THE ROLE OF GIZZARD SHAD (*DOROSOMA CEPEDIANUM*) IN EUTROPHIC FLORIDA LAKES

BY

Thomas L. Crisman

&

Helen M. Kennedy

Publication No. 64

Florida Water Resources Research Center

Research Project Technical Completion Report

Project Number A-041-FLA

Annual Allotment Agreement Numbers

14-34-0001-0110
14-34-0001-1110

Report Submitted: August 15, 1982

The work upon which this report is based was supported in part by funds provided by the United States Department of the Interior.

TABLE OF CONTENTS

ABSTRACT

The function of Dorosoma cepedianum (LeSueur) in Lake Eustis of central Florida was examined in three ways: short term stocking experiments, in situ algal viability studies, and simulation modeling of fish, phytoplankton, zooplankton, and phosphorus interactions. Fish were stocked in 7.07 m^2 tanks filled with lake water at natural densities of 42 g/m^2 (452 lbs/A) and at high densities of 125 g/m^2 (1331 lbs/A) in October 1979 and May 1980, respectively. In both experiments, the tanks were monitored for phosphorus and chlorophyll a concentrations, algal productivity, and phytoplankton and zooplankton densities. During the natural stocking density study, the fish were present for eight days, and during the higher stocking density study, the tanks were monitored for seven days with the fish present for the last four days of the study.

Results of tank experiments showed that gizzard shad had no impact on chlorophyll a values, productivity or phytoplankton densities in either short-term experiment. Gizzard shad caused a significant increase in both the concentration of orthophosphate and its ratio to total phosphorus in the natural stocking density study. The fish were also responsible for a significant decrease in copepod density during that study. During the high density stocking, the fish were not present long enough to affect significantly any of the parameters measured.

Additional experiments were conducted in November 1979 and August 1980 to test the viability of algae found in the feces of the fish. Feces were removed from the gizzard shad and incubated in filtered lake water contained in dialysis tubings that were suspended in Lake Eustis. After four days of incubation, several species of blue-green algae, particularly Chroococcus dispersus, Lyngbya contorta, L. limnetica, and Oscillatoria sp. were found to be viable.

The simulation model indicated that Lake Eustis is at steady state with a gizzard shad population so large and fecund that present shad removal practices have little impact on the fish population or the plankton community. The results of this investigation suggest that the presence of gizzard shad can promote lake eutrophication both through elevation of orthophosphate concentrations and differential digestion of diatoms and green algae thus increasing the competitive advantage of blue-green algae. This fish species does not appear to be a suitable candidate for use as a biocontrol agent for phytoplankton in eutrophic subtropical lakes.

ACKNOWLEDGEMENTS

Field studies were conducted at the Fisheries Research Laboratory of the Florida Game and Fresh Water Fish Commission in Eustis, Florida. Special thanks are extended to Bill Johnson and the staff of that facility. Dr. Katherine Ewel assisted in the development of the simulation model, Robert (Chip) Johnson aided in field experiments and laboratory analyses, and Lydia Gabelmann typed and assembled the final manuscript. We also wish to acknowlege James Bays, Daniel Campbell, Mary Gunn, Robert Knight, Floor Kooyman, David Rovel-Rix, and Phillip Sacco for sharing ideas and providing technical assistance throughout the study.

CHAPTER I. INTRODUCTION

Much of limnological research in the past two decades has concentrated on the causes, manifestations, and control of eutrophication. In the simplest terms, eutrophication may be defined as an enhancement of autotrophic production (algae and/or macrophytes) when supplied with elevated concentrations of some essential nutrient (usually phosphorus) considered limiting to photosynthesis. A broader view of eutrophication considers not only the structural and biomass response of autotrophic communities to increased nutrient addition, but also includes the total ecosystem response to such changes.

Eutrophication can be a natural process controlled by bedrock geochemistry, nutrient export characteristics of watershed vegetation, and lake morphometry, but it can also occur as the result of anthropogenic nutrient inputs from agriculture, industrial, and domestic sewage. Whatever the cause, eutrophication becomes a serious problem when a lake becomes so degraded that its utilization for agricultural, recreational or domestic purposes is impaired.

Problems associated with eutrophic lakes dominated by blue-green algae include an unpleasant taste and odor in municipal drinking water, death of livestock by ingestion and skin irritation to humans by contact with blue-green algal toxins, and a reduction of gamefish populations. Excessive macrophyte growth in streams and canals impedes navigation (as seen for the Panama Canal) and restricts flow thereby reducing both the efficiency of flood control and the delivery of water for irrigation and municipal consumption. Problems in lakes are largely recreational associated with problems in navigation of pleasure boats and a general stunting of gamefish populations.

Whether a eutrophic lake is dominated by either macrophytes or blue-green algae depends on the pre-impact condition of the lake and nutrient loading rates. Lakes that are shallow or possess extensive littoral zones with well developed macrophyte communities and are undergoing relatively slow rates of nutrient input tend to remain dominated by macrophytes under eutrophic conditions. Conversely, lakes whose pre-impact state was dominated by phytoplankton with poorly developed macrophyte communities (in part dictated by lake morphometry) will shift to blue-green domination with progressive eutrophication.

One can not always predict, however, how a lake will respond to eutrophication as evidenced by the example of Lake Apopka, Florida (Brezonik *et al.*, 1978). Prior to 1947, this lake was characterized

by extensive macrophyte development in spite of a progressive increase in nutrient input from agricultural and domestic sources. The macrophyte community was extensively damaged by a hurricane that struck the area in 1947. Due to high nutrient concentrations and the more rapid growth response of algae than macrophytes, the system quickly shifted to blue-green algal dominance. Today, more than 30 years later, submergent macrophytes are almost totally absent in the lake.

The first step in reversing the eutrophication of a lake is to determine whether the problem is the result of natural or anthropogenic processes. The greater the importance of human factors, the easier the task of restoration. Point-source anthropogenic nutrient inputs usually can be identified, quantified, and eliminated by installation of appropriate but costly waste treatment facilities. Non-point sources such as agricultural runoff are both harder to identify and to control.

Elimination of external nutrient inputs to a lake may not elicit a pronounced reduction in eutrophication. Nutrient release from organic lacustrine sediments enriched continuously for several years or decades through the accumulation of algal and macrophyte detritus may be sufficient to sustain high autotrophic production long after elimination of external nutrient inputs. Recognizing the real possibility that such lag times are likely to occur, several in-lake restoration techniques have been developed to either scavange nutrients from the water-column or to prevent the release of nutrients from organic sediments (Dunst et al., 1974). Most of these consider phosphorus to be the most likely nutrient limiting autotrophic production and have concentrated on reducing its availability.

The second major category of lake restoration techniques concentrates not on controlling nutrient availability but on the composition and biomass of autotrophic communities. It is conceivable that both the biomass and species composition of autotrophic communities can be altered thus reducing the deleterious effects of eutrophication on heterotrophic communities and ecosystem management without significantly altering nutrient concentrations in a lake. Nutrient concentrations do not define eutrophication, rather the process is defined by the biotic response to nutrient availability. The remainder of this paper addresses the feasibility of directly manipulating algal communities to reduce the problems associated with eutrophication.

PHYTOPLANKTON CONTROL

Management strategies for phytoplankton have concentrated on reducing both total algal biomass and the dominance of phytoplankton assemblages by blue-green algae. Little attention has been given to controlling individual algal species. While an increase in total phytoplankton biomass can lead to heterotroph community changes, especially for benthic invertebrates and fish, associated with a reduction in water-column oxygen levels through an increase in both nighttime respiration and decomposition, the most serious management problems arise when elevated algal biomass is coincident with a shift in phytoplankton dominance to favor blue-green algae. Several species of blue-greens produce toxins that cause skin irritations and gastro-intestinal problems for humans and are often fatal for both aquatic and terrestrial vertebrates ingesting toxin-ladened water. Additional problems include taste and odor problems in municipal water supplies and odors associated with the decomposition of floating blue-green scums windrowed along the lake shore.

Mechanical Control

Mechanical removal of phytoplankton biomass from the water column of a lake via filtration has never been considered seriously because of the cost involved with filtering large volumes of water coupled with the fact that algal populations have short turn-over times. Recently, however, Oswald (1976) and Koopman and Oswald (1977) have suggested that blue-green algal biomass in a lake can be drastically reduced by mechanically harvesting surface "scums" rather than the entire water column. They found that, due to their ability to control position in the water-column for maximum utilization of light, blue-green algal abundance at the surface (1 - 5 cm) of Clear Lake, California was concentrated relative to the whole water column by a factor of 100:1 to 2000:1. They suggested that the surface concentration-factor could be even greater near shore where windrows of algae are often concentrated by wind-induced currents.

Oswald (1976) considered several designs for a portable algal skimming unit to collect surface algal scums along the shore of Clear Lake and suggested that only 2% of the lake surface area would need to be processed in order to significantly reduce algal biomass in the entire lake.

The final harvestor design settled on by Koopman and Oswald (1977) consisted of a self-propelled barge whose bow was equipped with

a horizontal blade ("skim lip") used to collect water from the upper 7.6 cm of the water column. Algae were concentrated from lake water in a two-stage process consisting of a skimmer screen (74 - 105 μm mesh) and a continuously backwashed rotary strainer (microstrainer) whose mesh size was 44 - 61 μm. The collected algal scum was deposited in a compartment on the barge (750 L capacity) for eventual land disposal. Based on a comparison of chlorophyll concentrations from surface scums and collected algal slurry, a collection efficiency of 75% was calculated with a microstrainer mesh size of 44 μm. Total cost for mechanical control for Clear Lake was estimated to be $250/ha versus $200/ha for chemical control (copper sulfate). Oswald (1976) suggested that the cost of mechanical harvesting could be greatly reduced if a commercial market could be found for the collected algal slurry.

A number of problems exist with using mechanical harvesting for controlling phytoplankton biomass. Oswald (1976) stated that harvesting of surface algal scums, in order to significantly reduce algal biomass, would have to be performed continuously throughout the growing season due to both the fact that blue-greens would quickly re-concentrate at the surface as scums were harvested and the fast turn-over rates of algal populations during the growing season.

The mesh size (> 44 μm) used by Koopman and Oswald (1977) collected net plankton and totally missed nannoplankton (10 - 50 μm) and ultraplankton (< 10 μm). In addition, Karasik and Kondakov (1974) demonstrated that mechanical harvesting in a Soviet reservoir resulted in a shift in algal abundance and cell size from 2.5 X 10^6 cells/L dominated by net plankton (200-300 μm) to 22.0 X 10^6 cells/L dominated by nannoplankton (15 - 20 μm). Thus, mechanical harvesting either is totally inefficient at collecting nannoplankton or can break up filamentous and colonial net plankton into size-classes within the nannoplankton range. Because, for a given biomass, nannoplankton have higher productivity rates than net plankton associated with their greater surface/volume ratios and superior nutrient uptake kinetics (Kalff and Knoechel, 1978), total system productivity may be elevated following mechanical harvesting in spite of a removal of net plankton biomass.

Finally, while harvesting of algal scums may have been effective at reducing algal biomass in Clear Lake, California when only 2% of the lake surface was harvested (Oswald, 1976), such a limited effect may not achieve results elsewhere. Broad application of the technique to other systems is somewhat questionable due to interbasin differences in algal composition, the fact that not all species of blue-greens float, the failure to collect nannoplankton and ultraplankton, susceptability of

a lake to wind action, and the length of the shoreline relative to lake surface area.

Chemical Control

Chemical formulations for the control of algae fall into two general categories: algicides--chemicals that kill algae; and algistatics--chemicals that prevent algal growth. Most research has concentrated on controlling blue-green algae, especially dominant problem species, while having minimum effect on desirable species of diatoms and green algae. In select cases, species of the latter two groups have also posed problems (Fitzgerald, 1981).

Widespread chemical control of phytoplankton began in the late 1800s with the use of copper sulfate. It was discovered that blue-greens were more susceptible to copper toxicity than other algal groups, thus low concentrations of copper sulfate could be added to lakes for the selective control of blue-greens during "bloom" periods (Prescott, 1981). One draw-back with copper sulfate is the fact that the compound readily precipitates under the alkaline conditions characteristic of eutrophic lakes. Thus, any copper not immediately taken up by phytoplankton is lost to bottom sediments. This problem has been overcome in recent algicides through the use of two major organic chelates of copper, alkanolamines such as triethylanolamine and a mixture of citrate and gluconate of copper (Fitzgerald, 1981).

Potassium permanganate, a compound long used to control algal problems in water treatment plants, has also been used in the control of phytoplankton, but it must be applied at higher concentrations (0.5 - 4.0 mg/L) than copper sulfate (0.05 - 0.1 mg/L) to be effective (Fitzgerald, 1981). This compound is broader spectrum than copper sulfate and kills not only blue-greens but also problem green algae such as Dictyosphaerium.

Copper sulfate remains the most cost-effective chemical control for phytoplankton in large lakes, but as Fitzgerald (1981) points out, in smaller lakes and ponds cost is not as important a consideration as potential environmental problems associated with sediment enrichment of copper. The wide variety of organic compounds formulated after 1950 may be an effective control alternative in the latter situations. Many commercially available organic algicides utilizing phenylureas and substituted triazines such as simazine are effective at controlling algae in small ponds.

Aside from sediment accumulation of copper and its potential toxicity to aquatic heterotrophs, a number of problems must be addressed when proposing algicides for phytoplankton control. Not only should the product display specificity for particular algal groups or species without affecting other algae or heterotrophs, but its residence time in the water-column and degradability must be determined. It is important to note whether break-down products are potentially more toxic to non-target organisms than the parent compound and whether degradation rates, and hence effective treatment times, are comparable between different climatic zones.

Even if the above questions can be answered, secondary effects from algicide use can have a serious impact on lake ecosystems. Fish kills are often associated with water-column anoxia resulting from increased decomposition of phytoplankton eliminated by algicides. The problem becomes even more acute if toxin-producing blue-greens are the dominant phytoplankton, and if toxins reach critical levels following decomposition of the algae. Finally, algal dominance can shift either as the result of the elimination of superiorly competitive species or increased nutrient availability.

Although still in its infancy, an understanding of allelopathic interactions between algal groups or species may prove valuable in the future for controlling phytoplankton community structure. Extracellular metabolites including vitamins, proteins, carbohydrates, lipids, alcohols, and hormones are released into the water column by bacteria, algae, macrophytes, and zooplankton (Keating, 1981). Keating (1981) has documented that such extracellular products can lead to allelopathic interactions between aquatic biota, both plant and animal, that can either be positive (probiotic) or negative (antibiotic). Her paper provides an excellent historical review of publications dealing with allelopathy in aquatic systems.

Spring algal populations in many eutrophic temperate lakes are dominated by diatoms, and blue-greens dominate during summer. Keating (1978) examined the seasonal succession of algal dominance in eutrophic Linsley Pond, Connecticut for five successive years. She concluded that spring diatom abundance for a given year was inversely proportional to the population level of blue-greens for the previous year, especially during winter. Using isolates of the dominant blue-green and diatom species from Linsley Pond, she demonstrated that filtrates of the water in which blue-greens are cultured inhibited diatom growth. On the basis of both field and laboratory observations, she concluded that the magnitude and duration of spring diatom peaks in Linsley Pond were directly controlled by winter blue-green abundance and the associated

build-up of metabolic products and suggested that the spring diatom bloom in the lake could be enhanced by preventing winter-time blooms of blue-green algae.

Unfortunately, in related experiments in which algae were isolated from other eutrophic lakes of the region, Keating (1978) was unable to demonstrate the same interaction between blue-greens and diatoms. It appears that individual algal species display pronounced inter-basin physiological differences that strongly influence their response to allelopathic substances. Nevertheless, further research into the role of allelopathic interactions occurring in freshwaters may provide a new direction for the chemical control of phytoplankton populations.

Biological Control

Unlike for macrophytes, biological control of phytoplankton is in its infancy. A majority of the effort has been to propose that biological control may be feasible, but such statements are based solely on limited field observations and laboratory experiments. *In situ* demonstration of algal control is almost totally lacking. Research has concentrated on using pathogens and grazers as control agents.

Pathogens. Fungi show great promise for the control of macrophytes, especially free-floating taxa, but their potential for algal control is uncertain. A number of fungal parasites have been described for freshwater phytoplankton (Canter, 1954; 1973a) including blue-green algae (Canter, 1973b). Parasitism of algae is quite common in nature as demonstrated by the fact that 20% of over 500 actinomycete and fungal isolates studied by Safferman and Morris (1962) were antagonistic toward phytoplankton. The susceptability of algae to fungal attack may display a degree of species specificity that is directly related to the algal release rate of dissolved organic carbon (Masters, 1971). Unfortunately, little attention has been given to the use of fungi to control biomass or composition.

Viruses infecting blue-green algae (cyanophage or phycovirus) were first discovered by Safferman and Morris (1963). Subsequently, Safferman and Morris (1967) and Padan and Shilo (1969) noted that susceptable algal genera were never very abundant in nature where cyanophages were present and suggested that the virus was exerting control on the biomass level of phytoplankton.

Both the morphology and mode of infection are similar between bacteriophages and cyanophages reflecting the fact that both are

parasites of procaryotes (Dejardins, 1981). Once adsorbed to algal cells, cyanophages cause cell lysis, but as noted by Dejardins (1981) initial virus infection may not seriously affect algal photosynthetic rates. He also suggested that virus replication may occur only in photosynthetically active algal cells.

A number of questions remain regarding the role of virus in controlling blue-green algae. In a series of laboratory experiments Dejardins (1981) noted that the ability of cyanovirus to form plaques ("efficiency of plating") varied depending on the strain of the test algal species assayed. He further suggested that the use of cyanovirus for controlling natural algal populations could be hindered by the fact that temperate phages, those capable of forming lysogenic relationships with blue-green algae, could immunize cells against virulent forms of virus. Cannon (1975) suggested that lysogeny may permit survival of both virus and host at low densities during periods of environmental stress. When conditions improve (i.e. light, temperature, nutrient levels) and algal growth is stimulated, the virus may then be released and promote cell lysis.

Both Coulishaw and Mrsa (1975) and Dejardins (1981) noted that mutants of both cyanophage and algae often develop in laboratory cultures resulting in algae that are resistant to both the original and mutant cyanophages. Even under such conditions, a low-grade chronic viral infection was still observed.

Dejardins (1981) cautioned against direct application of laboratory observation to nature. While resistant strains of individual algal species will likely develop in nature, one cannot be assured that such strains will be as competitively superior as the original strain and be able to dominate the phytoplankton assemblage. It is also possible that the virus will evolve to form mutants that can infect the new algal strain.

Finally, the ability of cyanophages to control blue-green populations may be strongly temperature dependent. Safferman (1973) noted that certain strains of LPP-1 cyanophage were better able to form plaques when cultured at 26°C than at 35°C. The implications of these initial findings on the use of cyanophage for controlling blue-green algae in subtropical, tropical and shallow temperate lakes has not been investigated.

Most of the past research on cyanophage has concentrated on the physical, chemical, and biological properties of the virus. Large-scale field experiments are totally lacking. As pointed out by

Dejardins (1981), future research must be directed towards field testing as well as identification of a broad spectrum of cyanophages capable of controlling not only the initial bloom-producing algal species but also potential problem species that may assume dominance.

Given the fact that bacteria and blue-green algae are both procaryotes and hence closely related phylogenetically, the possibility exists that bacterial pathogens can be isolated that are specific to blue-greens while not affecting the remaining eucaryotic algae. A number of bacteria including Actinomycetes, Streptomyces, Bacillus, Pseudomonas, Cellvibrio, and Bdellovibrio produce substances that cause cell lysis in blue-green algae (Burnham, 1981), but the lytic substance is needed in high concentrations before it is effective. Burnham (1977) demonstrated that Bdellovibrio bacteriovorus could effectively control blue-green cultures through an autolytic dissolution of photosynthetic lamellae, but later (Burnham, 1981) questioned the in situ control potential of this bacterium because of the need to add large concentrations of protein to the culture medium in order to stimulate bacterial production.

It now appears that myxobacteria offer the greatest potential for the biocontrol of blue-green algae. Shilo (1967) first showed that myxobacteria caused cell lysis in several species of blue-green algae. Later, Daft and Stewart (1971) found that four myxobacteria could cause lysis in 40 strains of blue-green, but cell contact was necessary for lysis to occur. Cell lysis occurred within 2 - 7 days, and photosynthesis was reduced by 85% within 10 hrs following cell contact. Lysis appears to take place via dissolution of the mucopeptide layer of the cell (Daft and Stewart, 1973), and evidence suggests (Daft et al., 1975) that the efficiency of lysis increased with increasing water temperature.

Burnham (1981) isolated a myxobacterium, Myxococcus xanthus, that has been effective at controlling the blue-green Phormidium luridum. Once attached to an algal cell, Myxococcus forms colonies (spherules) with the algal cell as the core. Additional algal cells are entrapped by fimbriae (Dobson and McCurdy, 1979) and stringy protrusions of lipopolysaccharide and eventually concentrated into the spherule core. Lysis of algal cells occurs via exoenzymes of the bacteria.

Myxobacteria in general and Myxococcus xanthus in particular display greater potential for blue-green algal control than previously investigated bacteria. Daft and Stewart (1971) suggested that myxobacteria have no host-specific requirements but are capable of controlling most major species of bloom-producing blue-greens. Algal

control is effective when bacteria:algal cell ratios are as low as 1:100,000, and the bacteria encyst during periods of reduced water temperature or blue-green abundance (Burnham, 1981). Thus, a low inoculum is needed for effective control, and the bacteria are persistent in the environment when prey densities are reduced. Finally, unlike Bdellovibrio bactivorous, which requires high concentrations of exogenous protein as a growth requirement, blue-green algal cells serve as the complete growth medium for Myxococcus xanthus (Burnham, 1981).

As with viruses, the use of bacteria for the control of blue-green algae is still in its early stages of development. The natural role of bacteria as biocontrol agents in lake ecosystems is poorly understood. Without adequate large-scale field studies, it is impossible to predict what impact the introduction of bacterial pathogens will have on natural populations of blue-green algae or the lake ecosystem as a whole.

Grazers. Birds, zooplankton and fish have been proposed for the control of algae via grazing. Van Duesen (1974) proposed that swans (Cygnus olor) could potentially control filamentous algae in fish ponds, but Schuytema (1977) questioned their use without considering their role as nutrient loaders and cyclers in aquatic systems. The diet of the lesser flamingo (Phoenicopterus minor) consists largely of the blue-green alga Spirulina platensis (Beadle, 1974) but because of its restricted distribution to saline lakes of east Africa, this species is of limited value as a biocontrol agent.

Zooplankton are the most important algal grazers in temperate lakes. Haney (1971, 1973) in a series of detailed in situ grazing experiments calculated that zooplankton during periods of peak abundance (late spring and summer) filtered the entire water volume of his eutrophic and oligotrophic Ontario lakes, respectively, 4.69 and 1.14 times daily.

Macrozooplankton (cladocerans and copepods) dominate the zooplankton assemblages of oligotrophic and mesotrophic temperate lakes but are replaced by smaller-bodied macrozooplankton and microzooplankton (protozoans and rotifers) in eutrophic systems. Within the cladocera, elimination of large daphnids and the replacement of Bosmina coregoni by the smaller Boxmina longirostris often accompanies cultural eutrophication of temperate lakes (Beeton, 1969). Kerfoot (1974) attributed this general reduction in cladoceran body size during eutrophication to a pronounced habitat reduction and eventual

elimination of cold-water picivorous fishes as a result of hypolimnetic de-oxygenation. Predation pressure on planktivorous fish species, the major size-selective vertebrate predators on zooplankton, would thus be reduced.

It is also likely that the species replacements observed within the macrozooplankton may be a reflection of the inability of select taxa to ingest and/or assimilate blue-green algae, while the increased importance of microzooplankton (ciliated protozoans and rotifers) in eutrophic lakes may reflect the increased availability of planktonic bacteria as a food resource (Porter et al., 1979; Beaver and Crisman, 1982; Crisman et al., 1981). Thus, macrozooplankton composition and dominance may be limited both by enhanced vertebrate predation and the inability to ingest and assimilate blue-green algae, while that of the microzooplankton reflects the increased abundance of alternative food resources (bacteria).

Brooks and Dodson (1965) suggested that in the absence of vertebrate predation large-bodied zooplankton should have a competitive advantage over small-bodied taxa because the former feed not only on a wider size-spectrum of algal cell sizes but also are more efficient at grazing the restricted size range fed upon by the latter. Thus, if the abundance of large-bodied zooplankton could be enhanced in a eutrophic lake via the selective elimination of planktivorous fish, could zooplankton prove effective at controlling problem algal biomass in temperate lakes?

Population enhancement of large-bodied Daphnia species following elimination of planktivorous fishes has resulted in dramatic reductions in algal biomass in several North American (Schindler and Comita, 1972; Shapiro, 1979) and European (Hrbacek et al., 1961; Hrbacek, 1964; Shapiro, 1979) lakes. The fact that algal changes were associated with an increase of large Daphnia may lend credence to the contention of Haney (1973) that, although large zooplankton in general are more efficient algal grazers than small zooplankton, large cladocerans are much more important grazers in temperate lakes than are copepods.

Shapiro (1979) suggested that the phytoplankton response to grazing is not unidirectional but depends on the community structure and species composition of the initial algal assemblage. For example, increased Daphnia abundance resulted in a shift in algal dominance from blue-greens to greens, chrysophytes, diatoms, and euglenophytes in Severson Lake (Schindler and Comita, 1972) and Wirth Lake, Minnesota (Shapiro, 1979), but the appearance of similar daphnid populations in Lake Washington (Shapiro, 1979), Clear Lake, California (Cook and Connors, 1963) and experimental ponds in Minnesota (Lynch, 1979) encouraged blue-greens, especially Aphanizomenon. Lynch (1980) noted

that Aphanizomenon flos-aquae, during periods of increased Daphnia abundance, forms dense colonies of "grass-blade" morphology and that such colonies disappear when Daphnia abundance declines. The mechanism for colony formation is poorly understood but is likely related to a build-up of biochemical substances released by Daphnia. Once large colonies are formed, Aphanizomenon is less susceptable to Daphnia grazing and can remain a dominant component of the phytoplankton assemblage.

As demonstrated for phytophagous fish, zooplankton grazing can encourage phytoplankton dominance by blue-green algae (Porter 1973, 1975). Porter has shown that, once ingested, several species of blue-green algae pass viably through zooplankton guts, picking up nutrients released during the assimilation of more readily digestable species of greens and diatoms. She has also suggested that some blue-greens are unpalatable to zooplankton grazers and are rejected prior to ingestion.

Even if algal biomass and/or species composition are altered as a result of zooplankton grazing, it is difficult to predict how algal productivity will be affected. In general, nannoplankton (< 64 μm) should have greater primary productivity per cell biomass than net plankton (>64 μm) due to their greater surface-to-volume ratio and its influence on nutrient uptake rates. Which of the two algal size classes becomes dominant during periods of intense zooplankton grazing determines the level of autotrophic productivity and is influenced both by the ability of zooplankton to graze a broad spectrum of algal cell sizes and shapes and the relative importance of unpalatable or undigestable blue-green algae in both the nannoplankton and net plankton components. In addition, it is possible that during the course of zooplankton feeding, large filamentous algae (net plankton) may be broken apart, thus becoming functional nannoplankton.

Several fish species including tilapia (T. mossambica, T. nilotica), silver carp (Hypothalmicthys molitrix), thickhead carp (Aristichthys nobilis), mullet (Mugil cephalis), milkfish (Chanos chanos), and gizzard shad (Dorosoma cepedianum) are at least partly phytophagous as adults and thus have been considered as potential biocontrol agents for phytoplankton. With the exception of shad and mullet, all of these species are exotic to North America. Tilapia mossambica feeds predominantly on filamentous algae and diatoms (Munro, 1967), but some diatom species may remain viable following gut passage (Hickling, 1960). Tilapia nilotica has been used to control Pithophora in ponds (Avault, 1965) and can readily digest blue-green algae with an assimilation efficiency approaching 70-80% of digested carbon (Moriarty and Moriarty, 1973).

Silver carp, native to China, have been introduced throughout Southeast Asia, the Middle East, and Europe both for algal control and fish production. At stocking rates of 450 and 1,350 kg/ha in experimental enclosures (6 m^2), Kajak et al. (1975) noted that zooplankton biomass was reduced by 78% and 94%, respectively, while phytoplankton biomass was reduced by 78% in both treatments.

In addition to a reduction in total biomass, both the composition and dominant cell size of the phytoplankton changed. The importance of blue-green algae decreased while that of dinoflagellates increased, and nannoplankton (< 64 μm) became dominant over net plankton (> 64 μm). Subsequent investigations of the ecosystem response of four Polish lakes to silver carp introduction (Kajak et al., 1977) indicated that algae were the dominant dietary component of the fish. The authors suggested that the silver carp does not readily assimilate blue-green algae although they are ingested, and in lakes dominated by blue-greens, fish predation on zooplankton is intensified.

The Chinese thickhead carp has been introduced into eastern Europe where it is reported to prefer diatoms and green algae although it will ingest blue-greens including Microcystis (Krupauer, 1971). Unfortunately, no data on the assimilation efficiency of this fish on blue-green algae are available. Two fish, mullet and milkfish, have been proposed for controlling algae in brackish lakes, but their wide-spread use is questionable because of inconclusive data for the former and an inability to tolerate low temperatures for the latter.

Gizzard shad (Dorosoma cepedianum) is the principal phytophagous fish species in North American lakes. This species is rarely found in oligotrophic lakes, but in eutrophic lakes of the southern United States such as Lake Apopka, Florida it can contribute greater than 80% of total fish biomass (Huffstutler et al., 1965). Young gizzard shad (< 30 mm) feed primarily on zooplankton, and the older fish utilize mainly phytoplankton with some selection for zooplankton when sighted (Bodola, 1966; Cramer and Marzolf, 1970; Drenner and McComas, 1978; Kutkuhn, 1957; Tiffany, 1922). Both Dalquest and Peters (1966) and Baker and Schmitz (1971) reported that at times organic detritus can also be an important food source for the gizzard shad.

All of the above mentioned food habit studies indicated that the predominant food items are green algae and diatoms, and some studies indicated a low presence of blue-green algae in the gut of the fish. Studies concerning the energetics of gizzard shad emphasize the importance of lipid storage as an energy resource especially for the winter months when feeding is minimal (Smith, 1971; Pierce, 1977).

Selection for diatoms would insure higher lipid storage, and Dalquest and Peters (1966) found a higher density of benthic diatoms in the intestines of shad than was present in the surface of the lake sediment.

While manipulation of zooplankton populations for the biological control of phytoplankton biomass and composition has been proposed for temperate lakes, its application in other climatic zones may be questionable. Crisman (1981) indicated that large-bodied species of Daphnia are rarely if ever found in subtropical Florida lakes regardless of trophic state. Instead, daphnid populations are represented by the smallest-bodied species found in North America, principally Daphnia ambigua. Thus, while the size range of algal cells grazed by Florida cladocerans may be restricted relative to temperate assemblages because of their smaller body size, the overall annual grazing impact in Florida may be greater due to higher average water temperatures (Burns, 1969). The mechanism responsible for the exclusion of large-bodied cladocerans from subtropical lakes is poorly understood, but their absence may discount the use of zooplankton for the control of phytoplankton.

In order for grazing to be an effective biocontrol technique for algae in eutrophic subtropical lakes, phytophagous fish may have to be utilized to reduce the abundance of the larger-sized net plankton that often dominate eutrophic phytoplankton assemblages and are not effectively grazed by the smaller-bodied macrozooplankton characteristic of such systems. While exotic fish species could be introduced into Florida for this purpose, the ecology of our principal native phytophagous fish species, gizzard shad, is so poorly understood that we can not predict whether this species could be utilized as an effective algal control agent. If gizzard shad should prove not to be effective algal grazers and exotic fish are proposed for introduction, basic ecological information is needed in order to predict: 1) whether shad will be eliminated, presumably from competition, from eutrophic Florida lakes following the introduction of exotic fish species such as happened in several Florida lakes following the establishment of Tilapia aurea (Anonymous, 1975), and 2) whether such a replacement can have a detrimental impact on the entire lake ecosystem.

In the present study, the effects of gizzard shad on algal productivity and composition and phosphorus cycling were examined through: (1) experiments in which shad were added to enclosures filled with lake water after which various chemical and biological parameters were monitored for a short period of time; (2) experiments to test the in situ viability of algae that had passed through the gut of the fish; and (3) a simulation model of the fish and its trophic interactions in Lake Eustis, Florida.

CHAPTER II. MATERIALS AND METHODS

Study Site

Lake Eustis is one of five eutrophic lakes comprising the Oklawaha chain of lakes in Central Florida (Figure 1). For the period 1977 - 1980 mean annual values for total phosphorus, soluble reactive phosphorus, and functional chlorophyll a were 0.097 mg/L, 0.019 mg/L, and 34.2 mg/m^3, respectively (Brezonik et al., 1981). Mean annual phytoplankton abundance was 2.4×10^5/mL with blue-green algae clearly dominating the phytoplankton assemblage all year. The colonial blue-green Microcystis incerta was the dominant species during fall, winter and early spring (September - March), but it was replaced by the filamentous blue-greens Lyngbya limnetica and Spirulina laxissima during spring and summer (April - August).

Capture and Transport of Fish

The fish used in the experiments were usually caught in Lake Eustis or the Lake Eustis Canal. Because shad migrate in schools, it was necessary at times to catch the fish from other locations including Lake Carlton or Haines Creek, a tributary of Lake Eustis. The tank and viability experiments were conducted at the Fisheries Research Laboratory of the Florida Game and Fresh Water Fish Commission at Eustis, Florida.

Gizzard shad were caught, with the assistance of Commission staff at the Eustis Lab, by electroshocking with DC current. Other investigators have successfully shocked the fish by this technique without pronounced injury (Smith, 1971; Pierce, 1977), but we had extreme difficulty in keeping the gizzard shad alive for greater than 15 minutes after collection. Clupeids are very sensitive fish and easily excited. When placed in a non-circular holding container, a fish would place its head in a corner and remain there. R. Drenner (pers. comm.) found that gizzard shad need to swim continuously and discovered that circular trash cans were the best form of container to use. Because of high temperatures and rapid death, attempts to keep the fish alive in the summer months were abandoned.

Adult gizzard shad in the Oklawaha lakes are highly infected with redspot (Aeromonas aquatica). When captured, they secrete

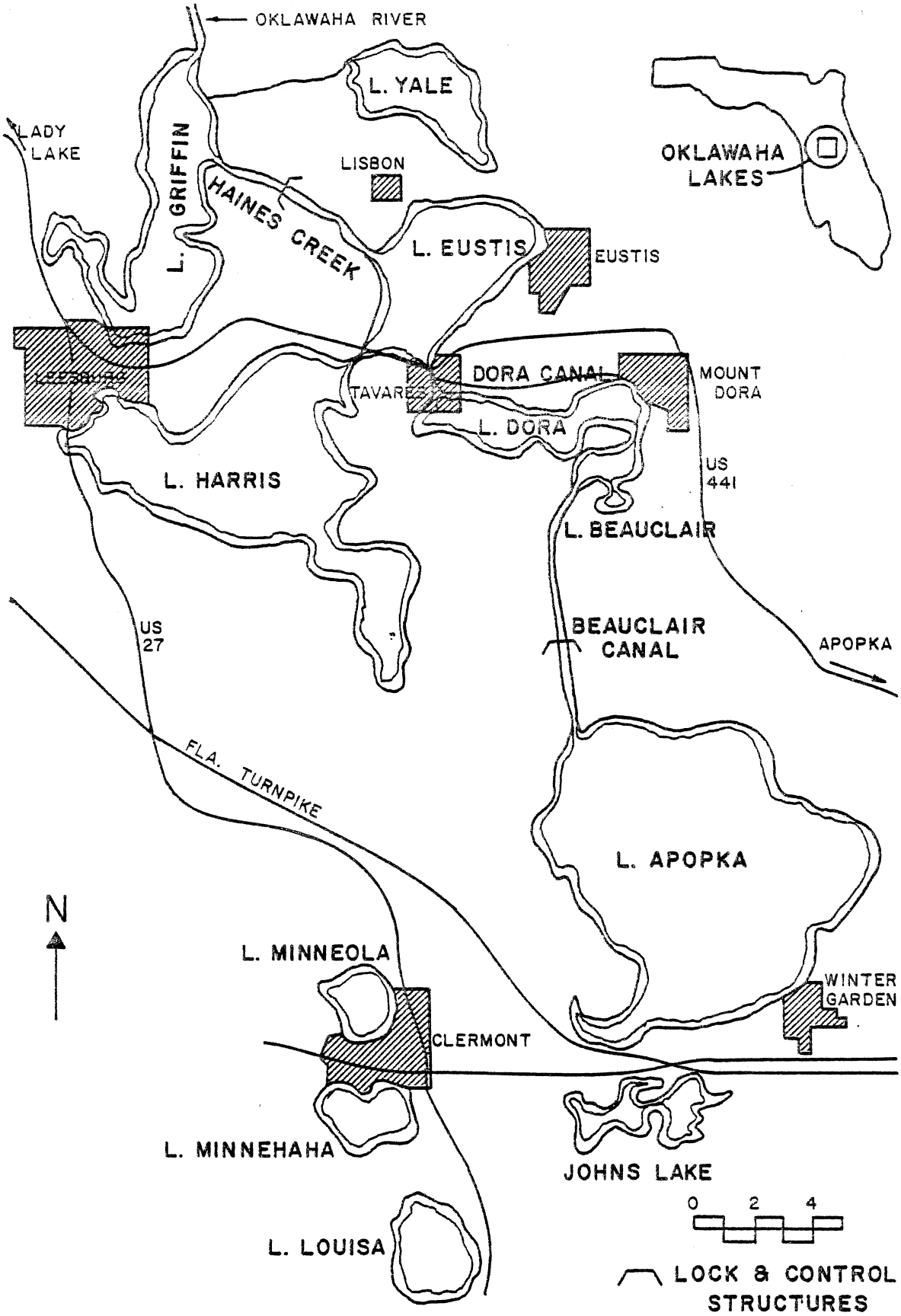

Figure 1. Lake Apopka and the Oklawaha chain of lakes.

excessive mucous over their bodies. Meinz (1978) found that survival of young American shad increased when they were transported in 4% salt (NaCl) solution. In subsequent collections we included treatment of the water in the round trash cans with a commercial product called Bait Saver which contains high concentrations of methylene blue. This increased the ionic strength of the solution. The fish were closely watched in the round containers, and any dead or dying fish were removed to avoid exciting the other fish.

In the laboratory, the fish were placed in large, ovoid, metal, flow-through tanks containing dechlorinated tap water (20-23°C), Bait Saver, and the antibiotic calfamiacin. If placed in a glass aquarium, the fish would either swim into a corner or bash their heads against the glass until they hemorrhaged and died. If the fish survived 24 hrs in the large metal tanks, they were much more likely to live long enough for the experiment.

Tank Experiments

Several investigators have used experimental enclosures in lakes or estuaries for *in situ* studies of the effects of consumers on primary producers (Andersson *et al.*, 1978; Cooper, 1973; Hulbert, 1972; Lamarra, 1975; McKellar and Obro, 1976; Porter, 1972). In this study, two experiments involving stocking gizzard shad in tanks were performed in order to investigate what effects the presence of the shad had on algal productivity and composition, and phosphorus concentrations.

The first experiment was conducted in October 1979 when fish were stocked at the natural density in Lake Eustis as estimated by Holcomb *et al.* (1977) of 42 g/m^2 (452 lbs/A). Huish (1957), however, estimated the shad population in Lake Beulah, Florida after addition of rotenone to be as high as 121 g/m^2 (1303 lbs/A). Consequently, in May of 1980 a second experiment was conducted, and the fish were stocked at 125 g/m^2 (1331 lbs/A).

Because of the enclosure size needed for the experiments, trouble in anchoring, and vandalism, it was more convenient to use large, circular fish tanks than lake enclosures for studying gizzard shad. Preliminary investigations with threadfin shad in similar tanks demonstrated that the fish can affect phytoplankton biomass in as quickly as two days. In order to prevent biasing experimental results by periphyton growth on the walls of the tanks, and because a rapid algal response was demonstrated, neither experiment exceeded eight days. The tanks measured approximately 1.2 m deep and 3 m in diameter and

were made of corrugated metal lined with blue plastic swimming pool liners. Six identical tanks were filled with water pumped from the Eustis Canal at least 24 hrs prior to the beginning of each experiment.

Gizzard shad for the October 1979 experiment were caught in Lake Eustis or in the canal and incubated inside the laboratory for at least 36 hrs after which they were transferred in round containers to the outside tanks. During the October experiment, two fish, with a combined mass of approximately 300 g (natural stocking density), were stocked in each of three randomly chosen tanks, and the remaining pools served as controls. The average mass of fish stocked at a higher density in the May study was 883 g. Again, two fish were introduced into each of three tanks, but they were of an older year class.

During the natural stocking-density experiment, various parameters (see below) were measured every two hrs for the first 24 hrs, and then once a day for the remaining seven days. The sampling schedule for the high stocking density experiment was different from that of the October study in two ways. Analysis of the October data showed that sampling every two hrs for the first day was not necessary. Thus, May sampling was done initially, two hrs after the fish were introduced, and twelve hrs later. The second change involved monitoring the tanks for three days prior to introducing the shad, then running the experiment for another five days with the fish.

The following chemical and physical parameters were measured for the tanks: conductivity, pH, temperature, orthophosphate, total phosphorus, and chlorophyll a. Conductivity and pH were measured at the beginning and end of each experiment, and periodically in between. Water temperature was measured at each sampling interval. For phosphorus analysis, two duplicated water samples were taken from opposite sides of each tank, and the four samples were averaged. Orthophosphate (soluble reactive phosphorus) and total phosphorus were analyzed by acid hydrolysis and colorimetric determination after USEPA (1974). Water samples for chlorophyll analysis were taken in triplicate from each tank. Volumes of 100 to 250 ml were filtered through 0.45 µm glass fiber filters, extracted with 90% acetone, and stored frozen until spectrophometric analysis was performed for concentrations of chlorophyll a and functional chlorophyll a (chlorophyll a - phaeophytin a) as in Standard Methods (APHA, 1976).

The following biological parameters were measured during the tank experiments: community metabolism, phytoplankton density, and zooplankton density. Community metabolism was measured in the tanks by three different methods. Diel oxygen determinations were made for the first 24 hrs after introduction of Dorosoma and during the last

24 hrs of each experiment after Odum and Hoskin (1958). Oxygen was analyzed by the Winkler method according to Standard Methods (APHA, 1976). During the October studies when diel oxygen measurements were not being taken, estimates of productivity were made by oxygen sampling at dawn and dusk (McKellar, 1975). During the May experiment, productivity was estimated on days other than those when diel measurements were taken by the light-dark bottle method as in Standard Methods (APHA, 1976).

Samples of phytoplankton were preserved in Lugol's solution and enumerated under an inverted microscope after Lund et al. (1958). Algae were identified to species where possible, using Prescott (1962) as a taxonomic reference, and zooplankton using Edmondson (1959).

Algal Viability Experiments

Velasquez (1939) investigated the viability of algae collected from the gut of gizzard shad. He partitioned the intestines into different segments, removed the contents from each section, and grew the algae in culture medium in the laboratory. Smith (1962) also cultured algae from various portions of the digestive tract of the fish, but, in an attempt to obtain a more natural growth medium, he grew the algae in "distilled water extract of soil." This study was concerned only with the viability of algae in the feces of the gizzard shad, and the algae were cultured in situ.

Viability experiments in the present study were conducted twice, November 1979, and August 1980. Fish for both experiments were collected by electroshocking. The feces were forced by hand from the anus by pressure placed along the lower digestive track. The feces were placed in dialysis tubing of pore size of 10,000 molecular weight, after Baskett and Lulves (1974). These bags contained the feces added to lake water that had been filtered through a 0.45 um fiberglass filter. All algal samples taken from the tubes were preserved with Lugol's solution, and were identified under a compound microscope (Prescott, 1962). For a comparison of algal consumption to algal viability, samples were also taken from the esophagus and gizzard of the fish in the August experiment and were preserved in formalin.

On the morning of November 16, 1979, twenty adult fish were caught in a canal draining into Lake Eustis. Individuals weighed between 550 and 1150 g, and about half of them did not have any feces in the hindgut. In order to insure a sufficient amount of feces, the fish

were grouped into four series of five fish each, and the feces obtained from each group were placed, respectively, into four dialysis tubes of 7 cm diameter each containing approximately 60 ml of filtered lake water. These tubes, along with four control tubes of filtered lake water, were suspended at approximately 0.25 m below the surface from a dock on Lake Eustis that extended 50 m into the lake. Algal samples were taken from each tube and from the lake at the initiation of the experiment. The tubes were incubated for four days at the in situ temperature of 19°C.

Studies performed by Vargo et al. (1975) on dialysis tubing showed that after four days at 20°C the passage of ions across the permeable membrane is significantly inhibited by the bacterial growth, and that by day 9, the bacteria have decomposed the membrane of the dialysis tubing. In order to insure unaltered nutrient exchange as well as algal succession, the tubes were removed from the lake after four days of incubation, and algal samples were collected.

On the afternoon of August 28, 1980, six fish were caught from Lake Carlton, three lakes upstream from Lake Eustis but still part of the Oklawaha chain. Lake Carlton was chosen as the site for fish collection because shad had not been observed in the Eustis canal for several days. After two hours of electroshocking, only six fish had been caught, but all contained feces. This was unlike the October study, where many of the fish, which were collected in the morning, had empty guts. Pierce (1977) also found that shad often had empty intestinal tracts in the morning. The fish were all adults between 600 and 1300 g each, and were divided into two groups of three fish each. As in the earlier experiment, samples were suspended at approximately 0.25 m below the surface from a dock on Lake Carlton and incubated for four days. Since average water temperature was 28°C, an extra control bag was incubated for each of the four days so the membranes could be checked each day by microscopic inspection for colonizing bacteria that might block nutrient exchange. Each of the six fish was dissected, and the contents of the esophagus and gizzard were collected for comparison with the fecal samples. All statistical analyses for the tank and viability phases of this investigation utilized the SAS (Barr et al. 1979) computer packages available through the Northeast Regional Data Center at the University of Florida.

Lake Eustis-Gizzard Shad Model

In order to enhance comprehension of the interactions of gizzard shad in the Lake Eustis system, a simulation model was developed to predict the effects the fish have on the algal assemblage and to investigate the impacts that removing the gizzard shad might have on the system. The model was written in Continuous Systems Modeling Program (CSMP) language and simulated on an IBM computer at the Northeast Regional Data Center, University of Florida.

CHAPTER III. RESULTS AND DISCUSSION

TANK EXPERIMENTS

A) Results

Conductivity and pH data are presented in Table 1. Specific conductance averaged between 220 and 232 μmho/cm in the October experiment when the shad were stocked at natural densities (42 g/m^2). In the May study, when the fish were stocked at high densities (125 g/m^2), conductivity averaged between 253 and 267 μmho/cm. The gizzard shad had no significant ($p < 0.05$) effect on the conductivity of the water (Tables 2 and 3). Differences between the October and May experiments correspond with the seasonal difference that Pollman et al. (1980) reported for Lake Eustis.

Throughout both experiments a significant increase ($p< 0.05$) in the pH of the water was observed (Table 2). In the natural stocking-density experiment the pH of the tank with fish was always significantly ($p <0.01$) higher than controls (Table 3). Throughout the experiment conducted in May with a high density of fish, there were slight yet significant ($p< 0.01$) differences between the average pH of the controls and those with fish (Tables 1 and 3). The one exception was on day 7 when all tanks had the same pH.

Graphs of changes in water temperature over time and the remaining parameters in Table 2 are presented in Appendix A. During the natural stocking density experiment average water temperature (Figure A-1) increased from 24°C to 25°C, but the change was not significant ($p < 0.05$). In the higher stocking density experiment of May, the average water temperature decreased (significant at $p < 0.05$) from 25.5°C to 23.5°C which was a result of continuous rainfall most of days 4, 5 and 6 (Tables 2 and 3).

Phosphorus

Throughout both experiments concentrations of total phosphorus (Figure A-2) varied between 0.03 and 0.09 mg/l, with no significant ($p < 0.05$) changes in or differences between any of the daily values. Analysis of variance for both experiments showed day to be the only significant factor affecting total phosphorus concentrations ($p < 0.01$).

Table 1. pH and conductivity during the tank experiments

Date	Fish pH	Fish Conductivity (μmho/cm)	Control pH	Control Conductivity (μmho/cm)
Natural Stocking Density October 1979				
Day 0	7.20	220	7.16	223
Day 2	7.10		7.03	
Day 4	7.53		7.46	
Day 8	7.36	232	7.29	232
High Stocking Density May 1980				
Day 0	7.06	253	7.09	260
Day 2	7.29		7.24	
Day 4	7.23		7.23	
Day 7	7.30	265	7.30	267

Table 2. Changes in parameters between day of stocking and the end of the experiment for tanks with and without shad. (+ = significant increase at $p < 0.05$; - = significant decrease at $p < 0.05$).

	Natural Stocking Density		High Stocking Density	
Parameter	Fish	Control	Fish	Control
Conductivity				
pH	+	+	+	+
Water temperature			-	-
Total Phosphorus				
Orthophosphate/ Total phosphorus	+	+		
Orthophosphate	+	+		
Chlorophyll a				
Functional chlorophyll a.				
Gross primary productivity				
Net primary productivity				
Algal density				
Chlorophyta				
Cyanophyta				
Diatoms				
Euglenophyta				
Algal volume				
Chlorophyta				
Cyanophyta				
Diatoms				
Euglenophyta				
Algal size class				
< 10µm				
10-20 µm				
20-30 µm				
30-50 µm				
> 50 µm				
Zooplankton density				
Cladocera				
Copepoda				
Rotifera				
Chaoborus sp.				

Table 3. Comparison of parameters in experimental tanks with fish to those in control tanks on the day of stocking and on the last day of the study. (+C = control tanks were significantly higher ($p < 0.05$); +F = tanks with fish were significantly higher ($p < 0.05$).

	Natural Stocking Density		High Stocking Density	
Parameter	Day 0	Day 8	Day 3	Day 8
Conductivity				
pH	+C	+C	+F	
Water temperature				
Total phosphorus				
Orthophosphate/ Total phosphorus				
Orthophosphate				
Chlorophyll *a*				
Functional chlorophyll *a*				
Gross primary productivity				
Net primary productivity				
Algal density				
Chlorophyta				
Cyanophyta				
Diatoms				
Euglenophyta				
Algal volume				
Chlorophyta				
Cyanophyta				
Diatoms				
Euglenophyta				
Algal size class				
<10 µm				
10-20 µm				
20-30 µm				
30-50 µm				
>50 µm	+C			
Zooplankton density				
Cladocera		+C		
Copepoda		+C		
Rotifera				
Chaoborus sp.				

The proportion of total phosphorus that is readily available for algal uptake was of particular interest. During the natural stocking density experiment, the percent of the total phosphorus that was orthophosphate (Figure A-3) increased significantly ($p < 0.05$) in both treatment and control tanks (Table 2), but there was never any significant differences ($p < 0.05$) between the two (Table 3). Analysis of variance of these data, however, showed day to be significant at $p < 0.01$, fish at $p < 0.05$, and tank at $p < 0.07$.

Orthophosphate was 40 to 70% of the total phosphorus in the experimental tanks throughout the high stocking density study (Figure A-3). No significant ($p < 0.05$) changes within or differences between tanks were noted. Analysis of variance for these data showed tank to be significant at $p < 0.05$.

During the natural stocking density experiment of October, the concentrations of orthophosphate (Figure A-4) oscillated between less than 0.01 mg/l and 0.03 mg/l until day 8 when they reached high levels of 0.036 mg/l in the tanks with shad and 0.057 mg/l in the control tanks. This increase was significant ($p < 0.05$) for both treatment and controls (Table 2), but there were no significant differences between the two. Analysis of variance showed all three factors (day, tank, fish) to be significant at $p < 0.01$.

Values of orthophosphate oscillated between 0.02 mg/l and 0.045 mg/l during the experiment where shad were stocked at high densities (Figure A-4). There were no significant ($p < 0.05$) changes in the values or differences between controls and treatments.

Chlorophyll a

In the experiment where shad were stocked at natural densities, concentrations of chlorophyll a ranged between 5 mg/m^3 and 15 mg/m^3 (Figure A-5). There were no significant ($p < 0.05$) changes in chlorophyll a concentrations during the experiment. There were also no significant ($p < 0.05$) differences between tanks with fish and control tanks.

During the higher stocking density experiment, average concentrations of chlorophyll a decreased from 11.5 mg/m^3 in the tanks with fish and 8.8 mg/m^3 in the controls to less than 6 mg/l in both treatments by the end of the experiment (Figure A-5). This decrease, however, was not significant ($p < 0.05$), and there were no significant differences between treatment and control tanks. Analysis of variance showed all three factors (day, tank, fish) to have a significant effect

on chlorophyll a concentrations ($p < 0.05$). Concentrations of functional chlorophyll a (Figure A-6) followed the same patterns as chlorophyll a, and analysis of variance showed the same results as it did for chlorophyll a.

Productivity

Gross primary productivity (Figure A-7) values for both control and experimental tanks were not significantly ($p < 0.05$) different during the natural stocking density study. Analysis of variance showed day to have a significant effect on net primary productivity (gross productivity-respiration), but not on gross productivity (Figure A-8).

Results for the high stocking density experiment are not conclusive, because even though the shad were not added until day 3, on day 2 the average productivity for the treatment tanks varied significantly ($p < 0.01$) from the controls. High variance between tanks regardless of presence or absence of shad makes it difficult to detect the effects of the fish on both gross and net primary productivity.

Dominant Algae

The dominant algal forms were identified to genus and species when possible and were analyzed in terms of density (#/ml), estimated volume, and cell size categories. A list of the dominant algae for the natural stocking density study is presented in Table 4. Total average phytoplankton densities (Figure A-9) did not vary significantly ($p < 0.05$) from initial conditions throughout the duration of the experiment in either the control tanks or the tanks containing gizzard shad, nor was any significant difference between treatment tanks and controls for either day noted. While the abundance of Chlorophyta in the tanks with fish remained essentially the same during the study, a slight but non-significant decrease in densities of green algae was observed in the control ponds. Increases in the densities of the Cyanophyta and Euglenophyta in both treatment and controls were not significant at $p < 0.05$. Densities of diatoms increased in the control tanks and decreased in the treatment tanks, but these differences were not significant ($p < 0.05$).

The dominant algae from the high stocking density study are listed in Table 5. Total phytoplankton numbers increased (Figure A-9) in both control and treatment tanks during the experiment but not significantly at $p < 0.05$. Increases in the density of Chlorophyta,

Table 4. Dominant Phytoplankton from the October 1979 tank experiments.

CHLOROPHYTA
Ankistrodesmus falcatus
Crucigenia tetrapedia
Scenedesmus abundans
S. alternans
S. quadricauda
Selenastrum capricornutum
S. sp. (colonial)
CHRYSOPHYTA (Diatoms)
Diatoma sp. (3 kinds)
Navicula sp. (2 kinds)
CYANOPHYTA
Botrycococcus sp.
Chroococcus dispersus
C. limneticus
EUGLENOPHYTA
Phacus sp.

Table 5. Dominant Phytoplankton from the May 1980 tank experiments.

CHLOROPHYTA
Ankistrodemus falcatus
Crucigenia tetrapedia
Dinobryon sps.
Scenedesmus abundans
S. alternans
S. bijuga
Selenastrum capricornutum
S. sp. (colonial)
CHRYSOPHYTA (Diatoms)
Diatoma spp. (3 kinds)
Navicula spp. (2 kinds)
CYANOPHYTA
Botrycococcus sps.
Chroococcus dispersus
C. limneticus
EUGLENOPHYTA
Phacus spp.

Euglenophyta, and Cyanophyta occurred both in tanks with and without Dorosoma. At the beginning of the experiment, however, the average density of Cyanophyta was significantly greater ($p < 0.05$) in the controls than in the fish treatments. Diatom densities remained low in all tanks throughout this experiment.

Changes in the volume of the dominant algae were also investigated. An average volume for each dominant alga was estimated from microscopic measurements for cell area. These values were used to calculate cell volume by the mathematical formula which best approximated the shape of the given alga. The value for volume was subsequently multiplied by the density for each species to get the total volume contributed by each alga.

At the initiation of the natural stocking density experiment, the Chlorophyta contributed a majority of the algal volume in both control and treatment tanks, with Cyanophyta and Euglenophyta being minor components (Figure A-11). By the end of the study, the total volume of algae in the control tanks had decreased, but not significantly ($p < 0.05$), while it hardly varied at all in the fish tanks. There were no significant differences ($p < 0.05$) between the tanks with shad and those without.

In the experiment where the shad were stocked at higher densities, total algal volume increased (Figure A-12) in both control and fish tanks, but this increase was not significant ($p < 0.05$). In general, the volume of Chlorophyta increased in both tanks with and without Dorosoma. The Euglenophyta decreased in the fish tanks but remained unchanged in the controls, and the blue-green algae increased in both treatments. The volume of diatoms remained low throughout the May experiment as did the density. None of these changes were statistically significant ($p < 0.05$).

In order to determine if Dorosoma cepedianum had any effect on the size of filamentous or colonial algae that might be consumed or passed through its gut, the dominant algae were divided into size classes. Since all of the dominant forms were nannoplanktonic, the algae were grouped into the following categories: < 10μm, 10-20μm, 20-30 μm, 30-50 μm, and > 50 μm.

During the natural stocking density experiment, there was an increase in the number of smaller phytoplankton (< 30 μm) and a decrease in the larger forms (30-50 μm, and > 50 μm) in the control tanks (Figure A-13), with the decrease in the largest category being significant at $p < 0.01$ (Table 2). In the ponds that contained fish, the only change was a slight decrease in the 10-20 μm range. In

Table 6. Zooplankton from the tank experiment.

COPEPODA	CLADOCERA	ROTIFERA
	Natural Stocking Density (October 1979)	
Diaptomus dorsalis	Bosmina longirostris	Asplanchna sp.
Cyclops sp.	Ceriodaphnia sp. (flat)	Brachionus angularis
Tropocyclops sp.	Ceriodaphnia sp. (round)	Brachionus budapestiensis
Copepodites	Diaphanasoma sp.	Brachionus calyciflorus
		Brachionus caudatus
		Brachionus havanaensis
		Filinia longiseta
		Keratella cochlearis
		Lecane luna
		Lepadella sp.
		Monostyla bulla
		Monostyla quadridentata
		Platyias sp.
		Polarthra sp.
		Trichocerca multicrinis
	High Stocking Density (May 1980)	
Diaptomus dorsalis	Bosmina longirostris	Platyias quadricornis
Cyclops sp.	Chydorus sphaericus	Brachionus havanaensis
Tropocyclops sp.	Ceriodaphnia sp. (flat)	Keratella quadrata
Copepodites sp.	Ceriodaphnia sp. (round)	Tricocerca sp.
Nauplii	Daphnia ambigua	Polyarthra vulgaris
	Diaphanasoma sp.	Platyias patulus
	Macrothrix rosea	

comparing the size class distribution between controls and treatments, the density of the largest size class (> 50 μm), which was dominated by a colonial Selanastrum sp., was significantly higher ($p < 0.05$) in the control tanks at initial conditions (Table 3). No algae of this category were found in one of the fish treatment tanks. There were no other differences noted between the tanks with Dorosoma and those without.

When the fish were stocked at higher densities, increases in all size categories occurred in both controls and tanks with gizzard shad (Figure A-14), but at no time were there significant differences ($p < 0.05$). In the tanks containing Dorosoma, the increase in the 30-50 μm category from initial conditions to day 4 was significant ($p < 0.05$), but represented changes prior to gizzard shad introduction. No other algal size class changes were significant.

Zooplankton

Zooplankton were divided into the following groups for analysis: copepods, cladocerans, rotifers, and Chaoborus. Lists of the species identified for both experiments are presented in Table 6. Rotifers were dominant in both number of species and abundance (Figure A-15) during the natural stocking density experiment in October, which corresponded to their importance in Lake Eustis during October 1979 (Pollman et al., 1980). Although values were higher in the tanks with Dorosoma at initial conditions, these differences were not significant ($p < 0.05$). Likewise the decrease in the rotifer population in these tanks throughout the study was also not significant ($p < 0.05$). While copepod densities in the control tanks remained about the same throughout the experiment, a slight decrease was noted in the tanks with gizzard shad. Although this decrease from an average density of 102/1 at initial conditions to 31/1 on day 8 was not significant ($p < 0.05$), the decrease was important enough to be different from the control tanks. Densities in the control tanks were significantly higher ($p < 0.05$) on day 5 and on day 8 than in the fish tanks. There was a high degree of variation in the genera of copepods present in tanks with and without shad, making it difficult to observe trends. Consequently, the only difference worth noting was the substantially lower density of Cyclops sp. in the treatment tanks than in the controls on day 8 ($p < 0.13$). Analysis of variance for these data showed tank to be significant at $p < 0.01$.

In the higher stocking density experiment copepods and cladocera increased in both treatments and controls (Figure A-16). The increase in copepod densities in the control tanks was significant at $p < 0.09$.

In tanks containing Dorosoma, the increase in copepods ($p < 0.08$) took place before the fish were introduced, between day 0 and day 3. Likewise, significant increases ($p < 0.02$) in Chaoborus densities in the tanks with fish occurred between day 0 and day 3. Values for Chaoborus were significantly higher ($p < 0.07$) at initial conditions in the control tanks (Table 3). Analysis of variance showed day to be the sole factor that had a significant effect ($p < 0.02$) on zooplankton concentrations.

B) Discussion

Seasonal Relationships

If the small tanks used for the experiments adequately simulate conditions in the lake, then certain seasonal differences that occur in Lake Eustis (as documented by Pollman et al., 1980) should occur also in the tanks. In May 1979, the average pH in Lake Eustis was 8.6 and in October it was 8.9. These values are notably higher than in the experimental tanks (Table 1), but this was probably due to lower production in the tanks than in the lake. In 1979, the average specific conductance for Lake Eustis was 291 µmho/cm with values for May and October being quite close. In the tanks, specific conductance was lower than in the lake, with the values for May being higher than October (Table 1). The low conductivity occurring in the tanks as opposed to the lake is an indication that the water in the canal which was pumped into the tanks is slightly different from the lake. Average surface temperatures for the lake were around 25°C in May of 1979 and about 27°C in October 1979. The values in the tanks were slightly cooler on the average (Figure A-1).

In 1979, Lake Eustis showed an average total phosphorus concentration of 0.17 mg/1 for May and for October an average of 0.05 mg/1, with orthophosphate being approximately 0.09 mg/1 and 0.01 mg/1, respectively. The concentration of total phosphorus in the experimental units varied between 0.02 mg/1 and 0.09 mg/1, with slightly higher values in May than October (Figure A-2). These values were somewhat lower in the tanks than in the lake in May. In the tanks during May, however, orthophosphate constituted a higher percentage of the total phosphorus than was generally observed in the fall study (Figures A-3 and A-4). This relationship correlates well with the ratio of orthophosphate to total phosphorus in the lake for the two seasons.

Pollman, et al. (1980) noted that chlorophyll a from the Oklawaha chain of lakes between 1977 and 1979 exhibited a great deal

of seasonal variation both between lakes and within a given basin. Over the three year period Lake Eustis was the least productive lake each year with a mean annual value for functional chlorophyll a of 36 mg/m^3 in 1979. In May of that year the average concentration for Lake Eustis was 37 mg/m^3 and in October it was 32 mg/m^3. The mean values for chlorophyll a in the tanks were notably lower than in the lake, more closely reflecting the levels in the canal. These lower pigment concentrations of 4 to 10 mg/m^3 chlorophyll a for the tank experiments are more indicative of a mesotrophic system than they are of eutrophic Lake Eustis.

In conjunction with the lower values of chlorophyll a for the tanks, average productivity and algal density were lower than estimated for Lake Apopka (no data were available on Lake Eustis but Lake Apopka has similar characteristics). No productivity values were reported for Lake Apopka in 1979, but Tuschall et al. (1979) reported average gross primary productivity values of 3.6 g C/m^2-day in 1977 and 2.98 g C/m^2-day in 1978. Even though Lake Apopka is more productive than Lake Eustis, empirical values varied greatly with season and weather on the day of sampling. Yet, the productivity values for the tanks were far lower than what one would expect from Lake Eustis, having a gross primary productivity that ranged between 0.15 g C/m^2-day and 1.5 g C/m^2-day (Figure A-7) with very little seasonal difference. Gross productivity in the May experiment peaked on day 2, took a sharp decline for the following three days that may have been related to almost continuous rain, and was followed by a slight increase as sunny weather prevailed on day 7.

Phytoplankton densities, as well as chlorophyll a values, were two orders of magnitude lower in the tanks than in Lake Eustis which averaged 2.10×10^5 organisms/ml during 1979 (Pollman et al., 1980). Although average algal densities for the lake during May and October, 1979 were very close to the annual average, species composition was different. The lake is dominated primarily by blue-green algae with three species -- Lyngbya limnetica, Microcystis incerta, and Spirulina laxissima -- displaying seasonal dominance. In Lake Eustis the Chlorophyta and Chrysophyta (diatoms) are subdominants with their highest values occurring in the fall.

Although the three dominant blue-green algae in the lake were present in the tanks, at no time were they dominant. The algal flora was dominated by Selenastrum and Scenedesmus (Tables 4 and 5) with the only cyanophyte of any importance being Chroococcus dispersus. Diatoms were noted in higher densities in the fall experiment which corresponded with their increase in the lake and the increase in silica values in the lake at that time (Pollman et al., 1980).

Total zooplankton densities in Lake Eustis were approximately 220 organisms/l in May 1979 and about 600 organisms/l in October (Pollman et al., 1980). Seasonal differences for the lake showed a higher abundance of copepods in the spring, with nauplii and copepodites being more numerous in the fall by almost 150 individuals/l. The abundance of rotifers in Lake Eustis was distinctly higher in the fall by almost 200 individuals/l than in May 1979. Pollman et al. (1980) did show that rotifer populations fluctuated in Lake Eustis on a monthly basis but in the tank experiments during October, large abundance of rotifers dwarfed the cladoceran and copepod communities by as much as 2000-5000 individuals/l. The average copepod and cladoceran densities in the ponds were more similar to those in the lake of roughly 50 individuals/l or less.

Zooplankton densities in the spring study were similar to the increased copepod and cladoceran densities in the lake. At the beginning of the May experiment, zooplankton densities were very low, but by the end of the experiment, they were roughly the same as those for Lake Eustis. Although zooplankton densities in the May study were similar to those in Lake Eustis, productivity and algal composition, which were the thrust of these investigations, were not similar to Lake Eustis in either October or May. Since these factors did not reflect the lake system, but more likely the canal off the lake, any conclusions drawn from the effects the shad had on these parameters during the tank experiments must be conservative.

Stocking Density and Short Term Effects of Gizzard Shad

The two most important factors concerning the fish in the tank experiments were the density of fish stocked and the length of time they were present for the experiment. The results presented in Tables 2 and 3 show that the shad caused no significant changes in these parameters when the fish were stocked at estimated natural densities (an average of 42 g/m^2) nor when they were stocked at high densities (125 g/m^2). Although the fish were stocked at a lower density in the October study, they were present in the tanks longer (total of eight days) than in the May experiment (total of four days).

Although variance between tanks was high in the natural stocking density experiment, the fish had an impact on orthophosphate concentrations, the orthophosphate to total phosphorus ratio, and on zooplankton densities. Increases in orthophosphate values and the

ratio of orthophosphate to total phosphorus occurred in both tanks with fish and control tanks (Figures A-3 and A-4), but analysis of variance showed the presence of fish had a significant effect on the values. The day of sampling and the tank were also significant factors ($p < 0.05$) that influenced both the concentration of orthophosphate and its ratio to total phosphorus. Consequently, the shad appear to cause a slight yet important increase in the orthophosphate concentration that is available for uptake by algae. This evidence supports the theory that consumers function as recyclers of nutrients. The significant increase of orthophosphate in the treatment tanks was not coupled, however, with any significant change in productivity due to presence of the fish. Productivity was higher in the stocked tanks than the control tanks at the end of the experiment, however. If the experiment had been of longer duration, perhaps the results would have shown a change in the other parameters.

At this natural stocking density, shad also had a significant effect on the copepod population (Table 3). High variance, however, made it impossible to discern if the fish were selecting for any species in particular. It is possible that the larger cyclopoids were selectively preyed upon by the fish (Drenner and McComas, 1978).

Because the shad did not affect either productivity or algal densities in October, and also because the gizzard shad populations were probably underestimated in the lake (Huish, 1957), in the spring of 1980 the fish were stocked at a higher density for the experiment. Analysis of variance of data for this experiment showed Dorosoma to have an important impact on both chlorophyll a values and the number of large algae of > 50 µm size, but no significant changes were noted between the day the fish were added and the end of the experiment (Table 2). No effect was seen on phosphorus nor the zooplankton values. Great variation between treatment and controls existed before the gizzard shad were even introduced, and it is likely that four days was too short a time for them to have a marked impact on the system. Had the fish remained in the tanks for a longer time, changes in phosphorus and zooplankton as well as productivity and algal composition may have been manifested. Delineating relationships between productivity and stocking density of Dorosoma proved futile because of the short duration of the experiments.

Extrapolation of the tank data to Lake Eustis is primarily limited to the results of the natural stocking density study. Although internal phosphorus loading by sediment resuspension is important (Pollman et al., 1980), evidence presented here suggests that the gizzard shad influence the orthophosphate levels to some degree. This may be seasonal, depending on the algae present and the success

the fish have in digesting them. The problem is, however, that the algal composition in the tanks did not accurately represent the lake where blue-green algae dominate.

Concerning the selection of copepods, two factors must be considered. In the October study, the fish were of year class zero, being 100 to 150 mm in length, and it has been noted that the young of the year shad (usually 30 mm or less) feed primarily on zooplankton (Cramer and Marzolf, 1970; Bodola, 1966). It is possible, but not likely, that these fish were in the process of switching their diet. The other factor is that because the ponds were less productive, visibility was greater than in the lakes, and the zooplankton were easier for the fish to see.

In summary, the length of time the gizzard shad were present in the tanks and high variance between the tanks within treatments and controls limit the reliability of the results. Given these constraints, these experiments indicate that the shad do not significantly affect primary productivity or algal composition at natural or at high density levels. After eight days, the fish (natural density levels) were shown to have an impact on orthophosphate concentrations and copepod densities. Differences in algal populations and productivity between the tanks and the lake make extrapolation to Lake Eustis possible, yet conservative.

Algal Viability Experiments

The results of the November experiment are presented in Table 7. On day zero, no algae were found in the filtered lake water controls. Although some algae were found in the fecal sample, few individuals were present. The dominant species found in the lake sample are marked by an asterisk in Table 7.

On the same day as this experiment, sampling for the limnological survey of the Oklawaha chain of lakes was conducted by the Department of Environmental Engineering Sciences, University of Florida, Gainesville. Their results showed that *Lyngbya contorta* made up 46% of the algal population, *Lyngbya limnetica* 21%, *Oscillatoria* sp. 1.2%, and *Scenedesmus quadricauda* 0.3%.

After four days of incubation, a few individuals of *Lyngbya limnetica* and *Oscillatoria* sp. were found in control samples; these probably were introduced to the bags either at the beginning of the experiment or at the time of collection of algal samples on the fourth day. *Chroococcus dispersus*, *Lyngbya contorta*, *L. limnetica*, and

Table 7. Algae identified from Lake Eustis Canal and algae cultured from feces of gizzard shad in November 1979. Samples 1-4 were controls and samples 5-8 contained feces. (x = present; xx = abundant; and * = dominant in lake sample.)

Algae Present in Canal	# ml	%	Day = 0 Controls 1	2	3	4	Day = 0 Samples 5	6	7	8	Day = 4 Controls 1	2	3	4	Day = 4 Samples 5	6	7	8
Chlorophyta:																		
Ankistrodesmus sp.	247	3.8																
Crucigenia crucifera	112	1.7																
C. quadrata	157	2.4																
C. tetrapedia	45	0.7																
Pediastrum simplex	22	0.3														x	x	
Scenedesmus alternans	381	5.8																
S. quadricauda	695	10.5														x	x	
**Selenastrum* sp.	2,311	35.0																
Euglenophyta																		
Euglena sp.	45	0.7																
Bacillariophyceae:																		
Melosira sp.	112	1.7																
Navicula sp.	67	1.0																
Cyanophyta:																		
**Chroococcus dispersus*	1,256	19.0					x	x							xx	xx	xx	xx
C. minutus	201	3.0																
Lyngbya contorta	90	1.4													x	x	x	x
L. limnetica	157	2.4							x			x			xx	xx	xx	xx
Merismopedia tenuissima	112	1.7													x			x
Microcystis aeruginosa	157	2.4																
Oscillatoria sp.	337	5.1					x	x		x			x	x	xx	xx	xx	xx
Detritus and sand							x	x	x	x					x	x	x	x

Oscillatoria tenuis were found in substantial numbers in all fecal samples of day four, and the latter two species were dominant. Merismopedia convoluta was found in two of the four samples but was not very abundant. Pediastrum simplex was found in two of the samples, but only a few individuals were present. It is probable that their survival was due mostly to chance since this species was not found consistently in all samples as were the other algae (Table 7).

The results of the August experiment are presented in Table 8. All the algae that were present in the lake sample were also found in the samples taken from the esophagus and gizzard of the fish. No attempt was made to quantitatively relate the proportion of algal species in the gut to that of the lake water, but, in general, it was about the same except for one species of Oscillatoria. There was a bloom of Oscillatoria sp. in Lake Carlton throughout the experiment, and although this alga was abundant in the esophagus and gizzard of the fish, its concentration never approximated that of the lake sample. Either the sample was not representative of the lake, or the fish had consumed their food in another lake and then migrated to Lake Carlton where the Oscillatoria bloom was present when the fish were collected.

At no time during the experiment was bacterial colonization dense enough to impair passage of nutrients across the membrane. All of the tubes were dipped in and out of the water three times each day to help minimize bacterial clogging of the membrane.

After the four-day incubation, several species of blue-green algae were found to be viable (Table 8). Of these, the only ones that were abundant were Chroococcus dispersus and Lyngbya contorta. Oscillatoria sp. was common, and the remaining taxa, including Scenedesmus quadricauda, were not observed in any great numbers.

The results of the two experiments are essentially the same, given that the species composition in the lakes varied seasonally. The gizzard shad are obviously more effective in assimilating some species of algae than others. The August experiment showed that the fish consumes whatever is available in the water column. This supports what others have found (Tiffany, 1921, 1922; Bodola, 1965; Jester and Jensen, 1972; Drenner and McComas, 1978).

Algae that can pass through the fish's gut and remain viable possess one main strategy for survival. This strategy is clear: they are not consumed by the predator. In the short term, by passing through the gut of the fish, the algae may pick up nutrients which are present in the gut and therefore gain increased productivity, as Porter (1976) showed for certain algae that pass through the gut of zooplankton.

Table 8. Algae identified from Lake Carlton compared with algae cultured from feces of gizzard shad in August 1980. Algae present in the gut were also identified. Samples 1 and 2 were controls and samples 3 and 4 contained feces. (x = present; xx = abundant; and * = dominant in lake sample).

Algae Present in Lake	# ml	%	Present in Esophagus & Gizzard Samples 3	4	Day = 0 Controls 1	2	Day = 0 Samples 3	4	Day = 4 Controls 1	2	Day = 4 Samples 3	4
Chlorophyta:												
Ankistrodesmus sp.	2,991	2.2	x	x								
Peridinium sp.				x								
Scenedesmus abundans	374	0.2	x	x								
S. alternans				x							x	x
S. quadricauda	1,496	1.1	x	x								
Bacillariophyceae:												
Melosira sp.			x	x								
Navicula sp.			x	x								
Cyanophyta:												
Anabaena sp.			x	x								
Aphanocapsa sp.	374	0.3	x	x								
Chroococcus dispersus	6,730	4.9	xx	xx							xx	xx
C. limneticus	748	0.6	x	x							x	x
Lyngbya contorta	1,869	1.4	xx	xx							xx	xx
Merismopedia tenuissima	748	0.6	x	x								x
**Oscillatoria* sp.	116,275	84.3	xx	xx							xx	xx
Spirulina sp.	5,608	4.1									x	x
Unknown filament											x	x
Zooplankton parts			x	x			x	x			x	x
Detritus and sand			x	x			x	x			x	x

However, the results of the short term stocking experiment did not show any significant increase in primary productivity due to the presence of gizzard shad. Although this viability experiment showed that some species of algae do survive passage through the gut of gizzard shad, radioactive tracer studies similar to those performed by Porter (1976) are needed to demonstrate whether or not those algae which pass through the gut pick up nutrients and therefore gain increased productivity.

The gizzard shad has dominated the fish biomass in the Oklawaha chain of lakes since the early 1950's, and most of the species of algae that presently dominate the photoplankton populations of these lakes can pass through the gut of gizzard shad and remain viable. This supports the theory that both the size of the gizzard shad population and the amount of time this fish has dominated the system have contributed to the success of the viable blue-green species. It is also possible that, in the cooler winter months, when one might expect to see a shift to green algae and diatoms as dominants, the gizzard shad are a substantial reason why these algae only become subdominant. Two contributing factors would be the viability of blue-green algae as well as the grazing effect that the shad have upon the green algae and diatoms. Consequently, even though the shad are indiscriminate in their feeding, they are affecting the phytoplankton composition of the Oklawaha chain of lakes through their ability to digest some species of algae more efficiently than others.

Lake Eustis - Gizzard Shad Model

The model is presented in Figure 2. All values of the state variables and their respective flows are expressed in grams C/m^2-month, with phosphorus flowing through the model with a molar ratio to carbon of 1:100. The values for algae, zooplankton, and phosphorus were obtained from Pollman *et al.* (1980), and estimates of the standing crop of gizzard shad were taken from Holcomb *et al.* (1977).

The rate equations for the model and the computer address of each are presented in Table 9. Explanations concerning the conversions of biomass to grams carbon, and information about the flows of carbon to and from their state variables are provided below.

The percent of the algal assemblage that was made up of the viable species was determined by assuming that all species of Cyanophyta were viable after passage through the fish's gut. Their average densities (in numbers/ml) were divided by the total average density for algae in Lake Eustis in 1979. The algae that were assumed to be indigestible

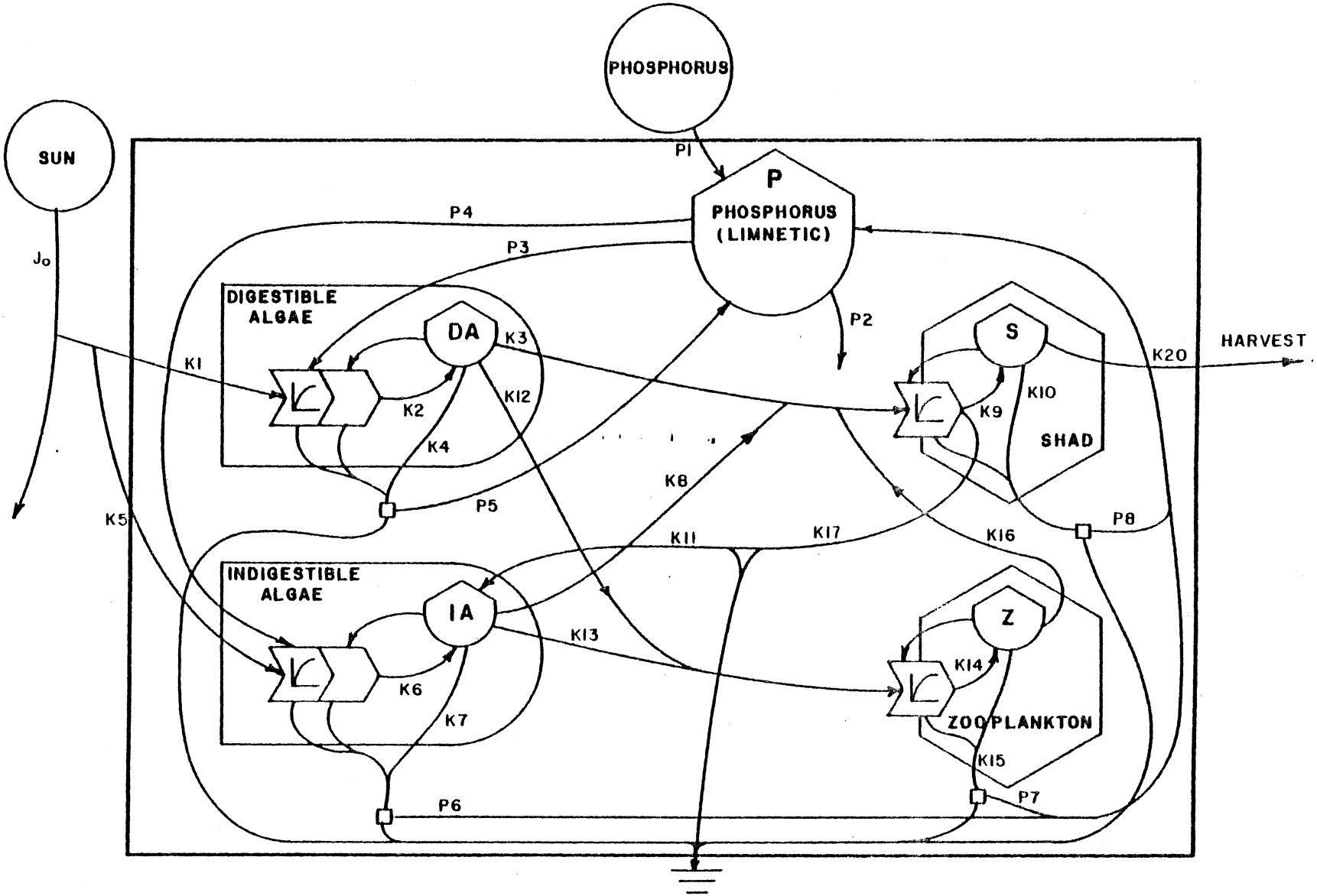

Fig. 2. Lake Eustis model. The state variables present are indigestible algae (IA), digestible algae (DA), gizzard shad (S), zooplankton (Z), and limnetic phosphorus (P).

were determined to constitute 77% of the 1979 algal assemblage, leaving 23% as digestible algae. Standing crop of algae was estimated by a conversion of chlorophyll a values to carbon. Summarizing others, Wetzel (1975) gave a range of carbon to chlorophyll a ratios between 20:1 and 66:1, and Paerl et al. (1976) reported a range from 3.7:1 to 50:1. Fontaine (1979) used a value of 25 mg C:1mg chlorophyll a for his model of Lake Conway, Florida, and this was the value used for the Lake Eustis model. The estimated carbon value was divided between IA and DA, based on the above percentages. For the flows (Table 9), long-term mean monthly solar radiation was put into a function named SUNLITE (see Appendix B). Gross primary productivity and respiration values were obtained from Pollman et al. (1980) and divided between the two algal compartments on the percentage basis stated above. Values of K1 and K5 were set at 1.0 in order to solve for K2 and K6, respectively. Losses of algae to gizzard shad were estimated to be ten times the values taken in by the fish based on the general theory of energy transfer up the food chain (Slobodkin, 1960). Losses to zooplankton were determined by difference to establish a mass balanced steady state at initial conditions.

Zooplankton biomass was estimated by multiplying the number of individuals by their respective dry weights as reported in Brezonik et al. (1969). A factor of 0.5 was used to convert biomass to carbon (Fontaine, 1979, based on personal communication from E.C. Blancher). Zooplankton were estimated to assimilate 43% of the phytoplankton (Comita, 1972). Loss of zooplankton to shad was estimated to be ten times that assimilated by the fish, and respiration of zooplankton was determined by difference.

Population estimates for gizzard shad, as for most schooling fish, have a large variance. The method of estimation that is considered to be most accurate is a "total kill" which is achieved for gizzard shad by selective poisoning with rotenone at small concentrations that are lethal to shad, but fairly harmless to other fish. When large scale selective poisoning to remove gizzard shad from lakes was done, consistently higher values of the population size of the fish were found than were anticipated. Bowers (1955) had estimated the population of shad in a pond to be 50 lbs/A, and after poisoning found the population to be 285 lbs/A. Huish (1957) estimated the population of Dorosoma cepedianum in a 5.3 ha lake in Florida, after addition of rotenone, to be as high as 1,303 lbs/A. Holcomb et al. (1977) estimated gizzard shad in Lake Eustis to be between 22 and 94 lbs/A.

Fresh weight values were converted to carbon by multiplying by 0.1 after Rodhe (1958). For simulation of the model, the following standing crops of shad were used: 0.24 g C/m^2 (22 lbs/A), 1.12 g C/m^2 (100 lbs/A), 3.9 g C/m^2 (350 lbs/A).

Table 9. Rate equations for model.

1A. Digestible Algae $\frac{dDA}{dt}$ = Gross production-respiration-predation

Pathway	Equation	Computer Address
Gross Production	$\frac{K_2 \cdot J_o \cdot DA}{(1+K_1 \cdot DA+K_5 \cdot IA)} \cdot P$	GPDA = ((K2*Jo*Da)/(1+K1*DA+K5*IA)) * (P/(HAFSAT+P)
Respiration	$K_4 \cdot DA$	RESPDA = K4 *DA
Predation by:		
Zooplankton	$K_{12} \cdot DA \cdot Z$	DAEATN = K3*DA*S + K12*DA*A
Shad	$K_3 \cdot DA \cdot S$	

1B. Indigestible Algae $\frac{dIA}{dt}$ = Gross production-respiration-predation

Pathway	Equation	Computer Address
Gross Production	$\frac{K_6 \cdot J_o \cdot IA}{(1+K_5 \cdot IA+K_1 \cdot DA)} \cdot P$	GPIA = ((K6*Jo*IA)/(1+K1+DA+K5+IA)) *(P/(HAFSAT+P))
Respiration	$K_7 \cdot IA$	RESPIA = K7*IA
Consumption by:		
Zooplankton	$K_{13} \cdot IA \cdot Z$	IAEATN = K8*IA*S + K13*IA*Z
Shad	$K_8 \cdot IA \cdot S$	
Viable Return from Shad	$K_{11} \cdot IA \cdot S$	VIABIA = K11*IA * S

Table 9 (Continued)

1C. Zooplankton $\frac{dZ}{dt}$ = Consumption-respiration-predation

Pathway	Equation	Computer Address
Consumption of:		
Phytoplankton	$K_{14} \cdot (IA+DA) \cdot Z$	ZEATS = ZLIM(IA+DA)*Z
Respiration	$K_{15} \cdot Z$	RESPZ = K15 *Z
Predation by Shad:	$K_{16} \cdot Z \cdot S$	ZEATN = K15*Z*S

1D. Gizzard Shad $\frac{dS}{dt}$ = Consumption-Viable passage-respiration-predation

Pathway	Equation	Computer Address
Consumption of:		
Phytoplankton and Zooplankton	$K_9 \cdot (DA+IA+S)$	SEATA = LIMEAT(IA+DA+Z)*S
Viable Passage of:		
Indigestible Algae	K_{17}	APASS = 1·1 * VIABIA
Respiration	$K_{10} \cdot S$	SRESP = K10*S
Predation by:		
People	$K_{20} \cdot S$	SHARV = K20*S

Table 9 (Continued)

1E. Phosphorus $\frac{dP}{DT}$ = Loading + Gains from Phytoplankton, Zooplankton, Shad - Uptake - Sedimentation

Pathway	Equation	Computer Address
Phosphorus	P_1 = Constant	PLOAD = P1
Sedimentation	$P_2 = K_{44} \cdot P$	POUT = P2*P
Gain from:		
Phytoplankton	$P_5 = K_4 \cdot DA \cdot K_{40}$	PIN = DAEXCR + IAEXCR + ZEXCR + SEXCR
Zooplankton	$P_6 = K_7 \cdot IA \cdot K_{40}$	DAEXCR = RATIO * RESPDA
Shad	$P_7 = K_{15} \cdot Z \cdot K_{40}$	IAEXCR = RATIO * RESPIA
	$P_8 = K_{10} \cdot S \cdot K_{40}$	ZEXCR = RATIO * RESPZ
		SEXCR = RATIO * SRESP
Uptake by:		
Phytoplankton	$P_3 = \frac{K_2 \cdot J_o \cdot DA}{(1+K_1 \cdot DA+K_5 \cdot IA)} \cdot P \cdot K_{40}$	PUPTAK = RATIO+GPDA + (RATIO+GRIA)
	$P_4 = \frac{K_6 \cdot J_o \cdot IA}{(1+K_5 \cdot IA+K_1 \cdot DA)} \cdot P \cdot K_{40}$	

*K_{40} is the ratio of phosphorus to carbon (see text).

Pierce (1977) reported an average gizzard shad consumption of 0.087 g/cm of fish-day. To get an average daily food consumption, this rate was multiplied by an average fish length of 20 cm. Pierce determined an assimilation efficiency of 42-58%, and a value of 50% was used for the model; carbon was considered to make up 50% of the material assimilated. The diet of the fish was then divided as follows: 69% indigestible algae, 21% digestible algae, 10% zooplankton.

Viable algae (VIABIA) that were returned to the IA compartment were estimated to be 41% of that lost to the shad, and the amount of algae that passed through the fish was considered to be 1.1 times the viable returned, or 45% of the loss of IA to shad. Respiration of shad was determined by difference, and the harvest of shad by humans was estimated from data obtained from the Fisheries Research Lab of the Florida Game and Fresh Water Fish Commission of Eustis, Florida.

Phosphorus loading was estimated from Fontaine (1979). Flows in and out of the phosphorus component were calculated using a ratio of phosphorus to carbon as previously stated. This factor is referred to as RATIO in Table 8 and Appendix B. The sedimentation flow was determined by difference. Phosphorus uptake by algae was represented by a Michaelis-Menten relationship, the half saturation constant varying with the concentration of phosphorus. This was simulated in a function called HALFSAT in which the constant was set at 0.025 for values of phosphorus less than 0.5 g/m^2, at 0.1 for values of phosphorus between 0.5 g/m^2 and 0.2 g/m^2, and at 0.3 for values greater than 0.2 g/m^2 P.

The lake model was initially run with the values calculated or estimated, as previously stated, at steady state conditions. Both phytoplankton compartments decreased rapidly, with their biomass approaching zero. This problem was corrected by three changes. The first was to place a limit on the amount of algae that a given biomass of fish could consume. This would simulate a feeding rate that has a point of saturation. This Michaelis-Menten relationship was represented in the function SHAD (Appendix B). For the same reasons, a similar limit was also placed on the zooplankton feeding, and the name of this function was ZOOP. Thirdly, a decrease was made in the rate at which algae were eaten by zooplankton (K12 and K13).

It was found that the phytoplankton standing crop was very sensitive to changes in the amount lost to zooplankton. A change in the values of K12 or K13 by as little as 0.05 (0.77%), when K12 = 6.45, would result in the respective algal population growing exponentially, stabilizing, or crashing. Such sensitivity could be a result of the simplicity of the model. Another aspect is that the only predation on zooplankton is by the gizzard shad, and there is no predation, other than the harvest by humans, upon the fish. Consequently, the lack of

these interactions, that occur higher in the food chain, could limit the ability of the model to describe the system.

Results of the simulations of the model after the adjustments were included are presented in Figures 3-5. In Figure 3, the initial condition of the shad biomass was 1.12 g C/m^2. The shad increased slightly, the digestible algae initially increased, but were cropped by the shad, and the viable algae increased and became dominant. Zooplankton increased to their carrying capacity, then stabilized. Phosphorus oscillated between 0.05 g/m^2 and 0.1 g/m^2. In Figure 4, the initial condition of shad was 3.92 g C/m^2 to simulated higher densities as reported by Huish (1957). This simulation caused the digestible algae to crash, the shad to decrease to around 2 g C/m^2 at the end of 2 yrs, and the indigestible algae to increase substantially. The simulation showed that zooplankton again reached carrying capacity, and phosphorus oscillated between 0.05 g/m^2 and 0.1 g/m^2.

Figure 5 presents the simulation with shad initial conditions of 0.25 g C/m^2 which was a low estimate given by Holcomb et al. (1977). In this simulation, the shad crashed, indigestible algae decreased after an initial rise, and digestible algae became dominant. The zooplankton and phosphorus behaved in the same way as in the two previous simulations. This simulation indicates that vast and permanent reductions in the shad population would lead to a shift in the algal composition in the lake.

In order to test the effects of controlling the shad population by harvesting, the addition of a removal rate (K20) to the natural density (1.12 g C/m^2) simulation was made. The amount of shad removed each year from Lake Eustis is small relative to the size of the population. The addition of the harvest resulted in little change in the simulation results without harvest (Figure 3).

These results would support the belief that the shad control program has essentially little or no effect upon the fish's population size in Lake Eustis. The fish migrate, however, between lakes in the Oklawaha chain, and in some of the smaller lakes, such as Beauclair, the harvest is more successful, removing more shad by weight per harvest as well as weight by area of lake. One reason for harvesting the shad from these lakes is an attempt to improve the sport fishery. Since the model did not include higher trophic levels, no inferences can be made of the effects the harvesting has on higher trophic levels.

The simulation of the model at the three different levels suggests that there is an ideal density of shad that Lake Eustis can support. This density appears to be somewhere between 1 and 2 g C/m^2 (100 to 225 lbs/A). The upper estimate that the Florida Game and Fresh Water Fish Commission had for Lake Eustis was 100 lbs/A, and the model

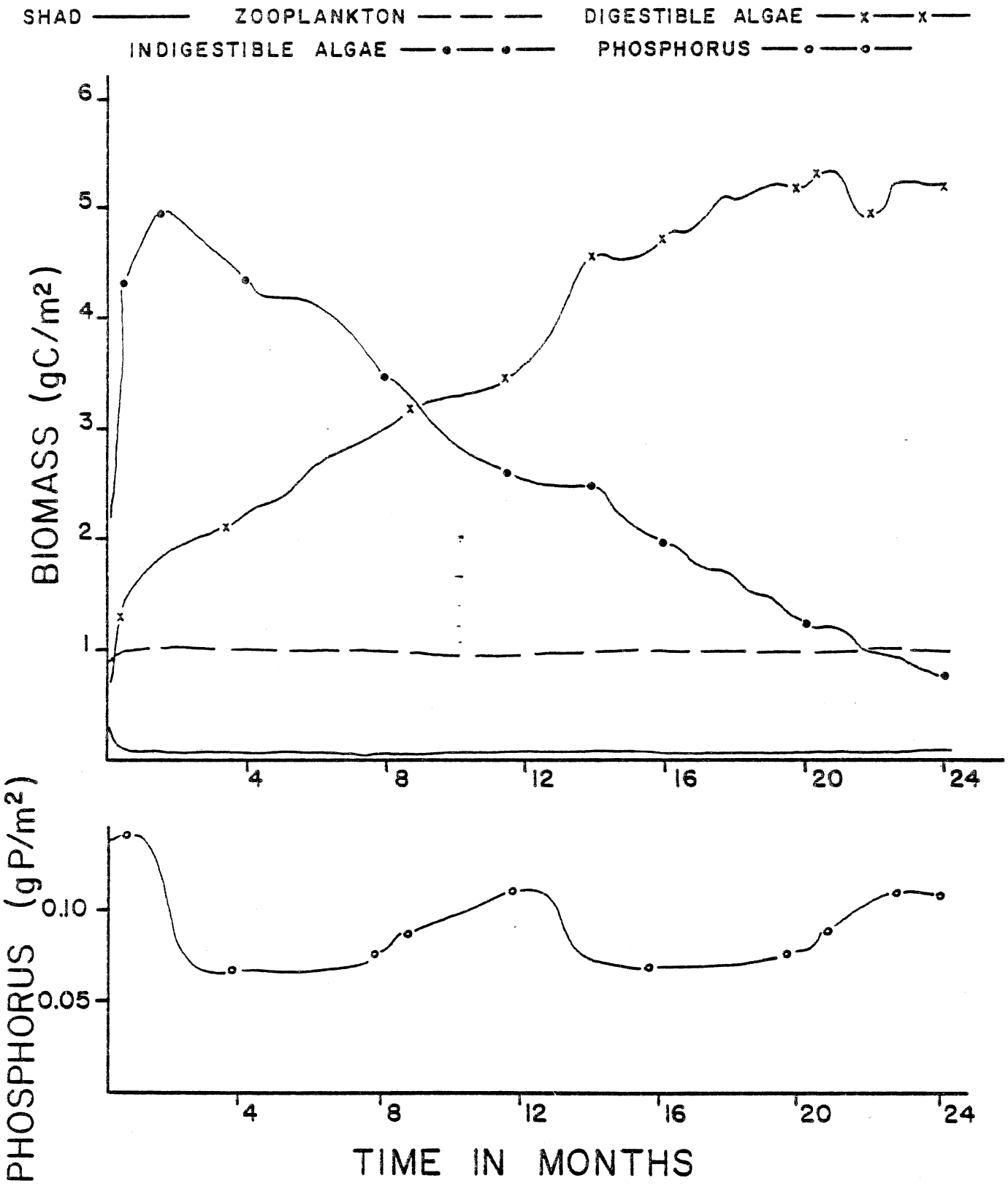

Fig. 3. Simulation of the Lake Eustis model with the initial condition of shad at natural densities of 1.12 g C/m^2.

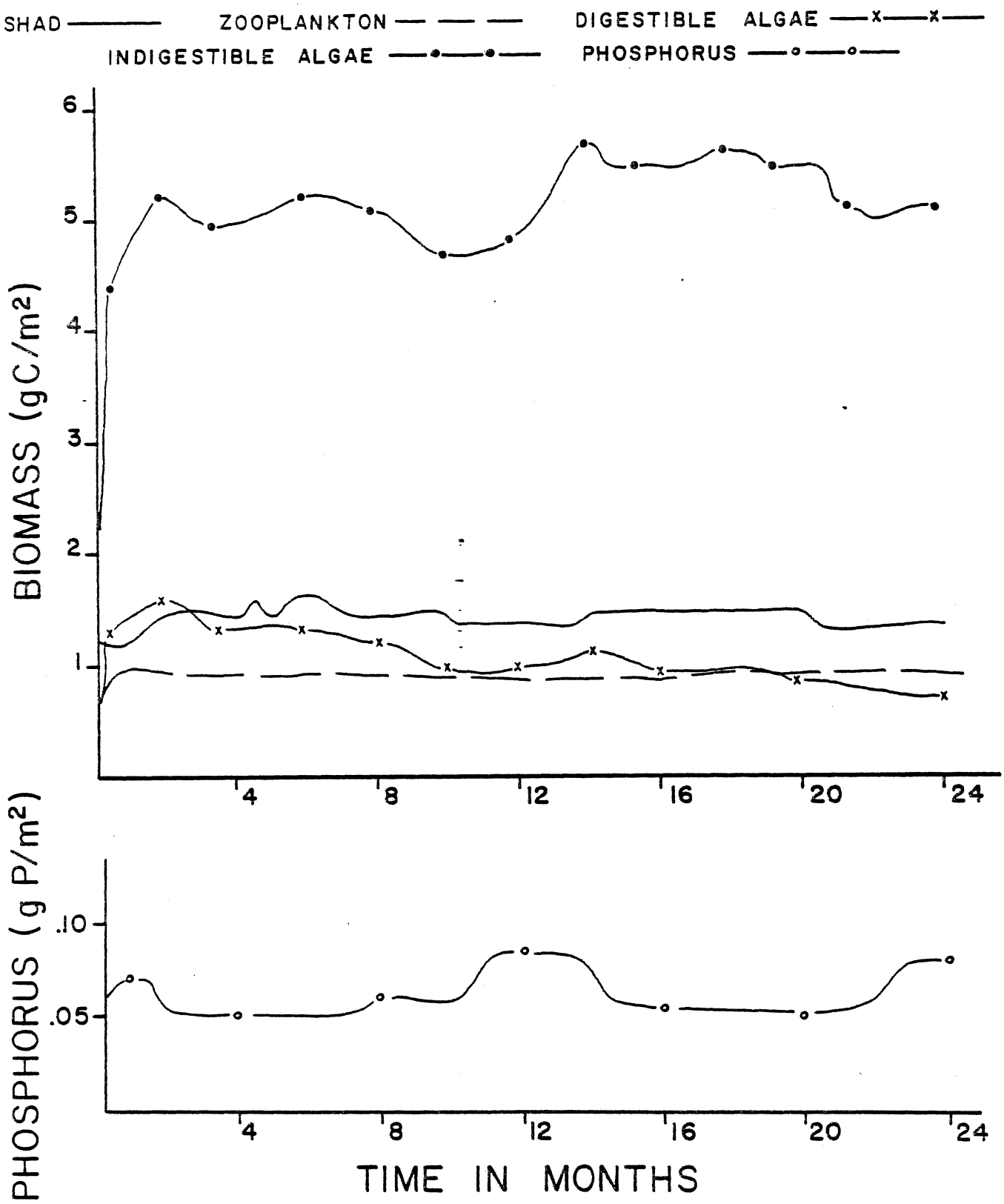

Fig. 4. Simulation of the Lake Eustis model with the initial condition of shad at high density of 3.92 g C/m^2.

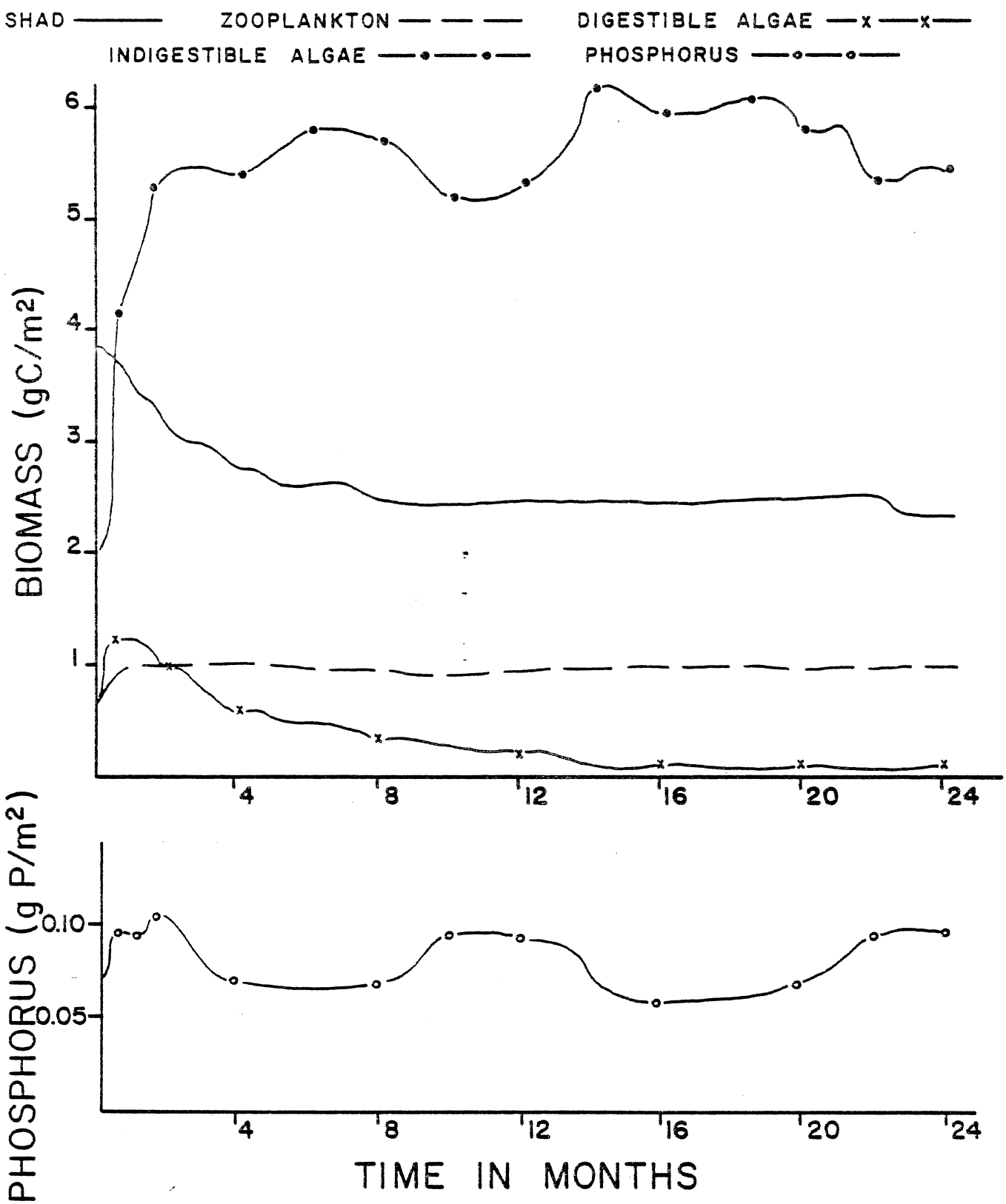

Fig. 5. Simulation of the Lake Eustis model with the initial condition of shad at low density of 0.25 g C/m^2.

suggests that values as high as 350 lbs/A cannot survive but will decrease until a steady state is reached. If predators had been included in the model, however, the gizzard shad population might have reached a steady state at a higher density than 2 g C/m^2. The model of low densities of the fish at the simulated algal composition resulted in the shad population being excluded from the system because there was not enough digestible algae available for net growth in the fish's population. The lake probably supports a higher gizzard shad population than the simulation model indicated because predators other than humans, along with migration and reproduction, are not included or adequately addressed in the model. The Lake Eustis model does support the theory that harvest by humans probably has little impact on the gizzard shad populations of the Oklawaha lakes.

CHAPTER IV. SUMMARY AND CONCLUSIONS

Eutrophication may be thought of as an enhancement of autotrophic production (algae or macrophytes) resulting from the increased availability of nutrients considered limiting to plant growth (usually phosphorus). The community structure, species composition, and overall abundance of all trophic levels can be altered as a result of elevated decomposition rates and resulting deoxygenation of the water column, a shift in algal dominance to favor unpalatable or toxin-producing blue-green algae, or a loss of habitat resulting from an alteration of the macrophyte community.

While large-bodied macrozooplankton, particularly Daphnia, have been proposed as effective agents for the biocontrol of algal populations in eutrophic temperate lakes, the presence of only small-bodied Daphnia species in Florida may hinder application of this technique in subtropical lakes. In such systems phytophagous fish may prove to be an effective alternative for phytoplankton control.

Although several exotic fish species could be introduced to control algae, the gizzard shad, Dorosoma cepedianum, is the only native phytophagous species that is commonly found in subtropical lakes. The present investigation was designed to collect basic ecological information on the influence of gizzard shad on nutrient availability and phytoplankton composition and productivity. The study was divided into three phases: 1) enclosure (tank) experiments, 2) algal viability following passage through gizzard shad guts, and 3) a simulation model of the role of gizzard shad in eutrophic Lake Eustis, Florida.

The tank experiments examined the short-term effects that natural and high densities of Dorosoma cepedianum have on water chemistry, phytoplankton and zooplankton. Although the fish were not present in the tanks long enough to have a measurable impact on phytoplankton productivity and composition, the gizzard shad did, after a period of eight days, cause an increase in the amount of orthophosphate in the water. Our data suggest that gizzard shad function as an important biotic cycler of phosphorus in eutrophic Florida lakes, but these data do not aid in determining whether such biotic nutrient cycling is as important a nutrient source for algae as that contributed by the physical resuspension of lacustrine sediments in these usually shallow lakes.

The algal viability studies indicate that shad readily digest diatoms and green algae while most species of blue-green algae remain viable after gut passage. Such differential digestion of algal taxa gives a competitive advantage to blue-green algae and insures their

continual dominance throughout the year even in winter when diatoms and green algae are often dominant in lakes of reduced trophic state. It is suggested that once shad become established in a lake, their differential grazing on phytoplankton causes a shift to blue-green dominance.

The simulation model suggested that Dorosoma cepedianum can affect algal composition either at high stocking densities in a short period of time, or perhaps at lower densities over a long period of time. The lake model also showed that attempts to control the gizzard shad population by harvesting probably do not have a great impact on the fish or the pelagic system. This study did not address the implications of shad removal on other fish species.

Due to the paucity of native fish species and the apparent ability of such species to promote blue-green algal dominance, the greatest potential for using fish for the biocontrol of phytoplankton in North America lies with the introduction of exotic phytophagous species capable of digesting blue-green algae. Widespread introduction of exotic fish species for the control of phytoplankton in North American lakes should be approached cautiously until detailed data regarding the possible introduction of exotic pathogens, interactions with native gamefish species, temperature and breeding requirements, and the ecosystem effects of fish grazing are available. It is essential to determine the dietary importance of algae, zooplankton, and detritus for each exotic fish proposed for introduction. Fish can alter phytoplankton composition directly both through their differential assimilation of select algal taxa, especially blue-greens, and/or selective predation on zooplankton, the principal invertebrate grazers of phytoplankton in freshwater lakes. Nutrient availability may be altered as a function of the total assimilation efficiency of the fish and a possible shift to small-bodied zooplankton possessing faster turn-over rates and thus a greater impact on nutrient cycling per body weight than larger-bodied taxa. Thus, fish grazing can also indirectly affect algal composition via an enhancement of the competitive ability of subdominant algal species in an altered nutrient pool.

REFERENCES

American Public Health Association. 1976. Standard methods for the examination of water and wastewater. 14th ed., APHA, Washington, D.C., 1193 p.

Andersson, G., H. Berggren, G. Cronberg, and C. Gelin. 1978. Effects of plantivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59:9-15.

Anonymous. 1975. Aquatic Biological Pollution in Florida. Nature 253: 238.

Avault, J.W., Jr. 1965. Biological weed control with herbivorous fish. Proc.South.Weed Conf. 18: 590-591.

Baker, D.C., and E.H. Schmitz. 1971. Food habits of adult gizzard and threadfin shad in two Ozark reservoirs. Reservoir Fisheries and Limnology Special Publication No. 8 of the Amer. Fisheries Society, 3-11.

Barr, A.J., J.H. Godnight, J.P. Sall, W.H. Blair, and D.M. Chilko. 1979. SAS user's guide 1979 edition, SAS Institute Inc.

Baskett, R.C., and W.J. Lulves. 1974. A method of measuring material growth in aquatic environments using dialysis culture. J. Fish. Res. Board Can. 31: 372-374.

Beadle, L.C. 1974. The Inland Waters of Tropical Africa. Longman. London. 365 pp.

Beaver, J.R. and T.L. Crisman. 1982. The trophic response of ciliated protozoans in freshwater lakes. Limnol. Oceanogr. 27: 246-253.

Beeton, A.M. 1969. Changes in the environment and biota of the Great Lakes. pp. 150-187. In: G.A. Rohlich (ed.). Eutrophication: Causes, Consequences, Correctives. Nation. Acad. Sci., Washington. 661 pp.

Bodola, A. 1966. Life history of the gizzard shad, Dorosoma cependianum (LeSueur), in western Lake Erie. U.S. Fish and Wildl. Ser. Fish. Bull. 65(2), 391-425.

Bowers, C.C. 1955. Selective poisoning of gizzard shad with rotenone. Prog. Fish. Cult. 17(3): 134-135.

Brezonik, P.L., W.H. Morgan, and E.E. Shannon. 1969. Eutrophication factors in North-Central Florida lakes. Univ. of Fla. Water Res. Research. Center Publ., 85 pp.

Brezonik, P.A., S.D. Preston, and T.L. Crisman. 1981. Limnological studies on Lake Apopka and the Oklawaha chain of lakes. 4. Water quality in 1980 and a summary of the four-year data base. Report No. ENV-07-81-02. Department of Environmental Engineering Sciences, University of Florida. 140 pp.

Brezonik, P.L., C.D. Pollman, T.L. Crisman, J.N. Allison, and J.L. Fox. 1978. Limnological studies on Lake Apopka and the Oklawaha chain of lakes. Rpt. #ENV-07-78-01. Dept. Env. Eng. Sci., University of Florida. 283 pp.

Brooks, J.L. and S.I. Dodson. 1965. Predation body size and composition of plankton. Science 150: 28-35.

Burnham, J.C. 1977. Bacterial control of aquatic algal populations. Proj. Complet. Rpt. 548. U.S. Dept. of Interior.

Burnham, J.C. 1981. The utilization of bacteria in managing cyanobacterial populations: a review and update. pp. 230-258. In: Proc. of Workshop on Algal Management and Control Tech. Rpt. #E-81-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. 313 pp.

Burns, C.W. 1969. Relation between filtering rate, temperature and body size in four species of Daphnia. Limnol. Oceanogr. 14:693-700.

Cannon, R. 1975. Field and ecological studies on blue-green algal viruses. pp. 112-117. In: P.L. Brezonik and J.L. Fox (eds.). Water Quality Management Through Biological Control. Rpt. #ENV-07-75-1, Dept. of Env. Eng. Sci., University of Florida, Gainesville. 164 pp.

Canter, H.M. 1954. Fungal parasites of the phytoplankton. III. (studies on British chytrids, XIII). Proc. Brit. Mycol. Soc. 37: 111-132.

Canter, H.M. 1973a. On Zygorhizidium venustum (Canter) n. comb. together with an illustrated list of chytrids occurring on chrysophycean algae. Nova Hedwigia 21:577-597.

Canter H.M. 1973b. A guide to the fungi occurring on planktonic blue-green algae. pp. 145-158. In: T.V. Desikachary (ed.). Taxonomy and Biology of Blue-green Algae. First Internat. Symp. on Taxon. and Biol. of Blue-green Algae, University of Madras, India.

Comita, G.W. 1972. The seasonal zooplankton cycles, production and transformations of energy in Severson Lake, Minnesota, Arch. Hydrobiol., 70:14-66.

Cook, S.F. and J.D. Conners. 1963. The short-term side effects of the insecticidal treatment of Clear Lake, Lake County, California, in 1962. Annal. Entomol. Soc. Amer. 56: 819-824.

Cooper, D.C. 1973. Enhancement of net primary productivity by herbivore grazing in aquatic laboratory microcosms. Limnol. and Oceanogr. 18:31-36.

Coulishaw, J. and M. Mrsa. 1975. Co-evolution of a virus-alga system. Appl. Microbiol. 29:234-239.

Cramer, J.D., and G.R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. Trans. Amer. Fish. Soc. 99:320-332.

Crisman, T.L. 1981. Algal control through trophic-level interactions: a subtropical perspective. pp. 131-145. In: Proc. of Workshop on Algal Management and Control. Tech. Rpt. #E-81-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. 313 pp.

Crisman, T.L., J.R. Beaver, and J.S. Bays. 1981. Examination of the relative impact of microzooplankton and macrozooplankton on bacteria in Florida lakes. Verh. Internat. Verein. Limnol. 21. 359-362.

Daft, M.J. and W.D.P. Stewart. 1973. Light and electron microscope observations on algal lysis by bacterium CP-1. New Phytol. 72:799-808.

Daft, J.J. and W.D.P. Stewart. 1971. Bacterial pathogens of freshwater bluegreen algae. New Phytol. 70:819-829.

Daft, J.J., S.B. McCord, and W.D.P. Stewart. 1975. Ecological studies on alga-lysing bacteria in fresh waters. Freshwat. Biol. 5: 577-596.

Dalquest, W.W., and L.J. Peters. 1966. A life history study of four problematic fish in Lake Diversion, Archer and Baylor Counties, Texas. Texas Parks and Wildlife Dept., 87 p.

Desjardins, P.R. 1981. Cyanophages - are they potential biological control agents of nuisance blue-green algae? pp. 198-229. In: Proc. of Workshop on Algal Management and Control Tech. Rpt. #E-81-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. 313 pp.

Dobson, W.J. and H.D. McCurdy. 1979. The function of fimbriae in Myxococcus xanthus-1. Purification and properties of M. xanthus fimbriae. Can. J. Microbiol. 25: 1152-2260.

Drenner, R.W., and S.R. McComas. 1978. Capture probability: The role of zooplankter escape in the selective feeding of planktivorous fish. J.Fish.Res. Board Can. 35: 1370-1373

Dunst, R.C., S.M. Born, P.D. Uttormark, S.A. Smith, S.A. Nichols, J.D. Peterson, D.R. Knaver, S.L. Serns, D.R. Winter, and T.L. Wirth. 1974. Survey of lake rehabilitation techniques and experiences. Tech. Bull. #75, Wisconsin Department of Natural Resources, Madison. 179 pp.

Edmondson, W.T. (ed). 1959. Freshwater biology. John Wiley and Sons, Inc., New York, 1248 pp.

Fitzgerald, G.P. 1981. Selective algicides. pp. 15-31. In: Proc. of Workshop on Algal Management and Control Tech. Rept. #E-81-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. 313 pp.

Fontaine, T.D. III. 1979. Community metabolism patterns and a simulation model of a lake in Central Florida. Ph.D. Dissertation, University of Florida, Gainesville, 415 p.

Haney, J.F. 1971. An in situ method for the measurement of zooplankton grazing rates. Limnol. Oceanogr. 16: 970-977.

Haney, J.F. 1973. An in situ examination of the grazing activities of natural zooplankton communities. Archiv. Hydrobiol. 72: 87-132.

Hickling, C.F. 1960. The Malacca tilapia hybrids. J. Genet. 57:1-10.

Holcomb, D.E., W.E. Johnson, J. Jenkins, J. Bitter, and L. Prevatt. 1976. Upper Oklawaha basin fisheries investigations. Third annual performance report. Dingell-Johnson Project F-30-3. Florida Game and Fresh Water Fish Commission.

Holcomb, D.E., W.E. Johnson, J. Jenkins, J. Bitter, and L. Prevatt. 1977. Oklawaha fisheries basin studies. Florida Game and Fresh Water Fish Commission Publication.

Hrbacek, J. 1964. Contribution to the ecology of water-bloom-forming blue-green algae Aphanizomenon flos-aquae and Microcystis aeruginosa. Verh. Verein. Limnol. 15: 837-846.

Hrbacek, J., M. Dvorakova, M. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Internat. Verein. Limnol. 14: 192-195.

Huffstutler, K.K., J.E. Burgess, and B.B. Glenn. 1965. Biological, physical, and chemical study of Lake Apopka, 1962-1964. Florida State Board of Health, Jacksonville. 78 pp.

Huish, M.T. 1957. Studies of gizzard shad reduction at Lake Beulah, Florida. Proceeding of 11th Annual Conf. of the S.E. Assn. of Game & Fish Commissioners. 66-70.

Hurlbert, S.H., J. Zedler, and D. Fairbanks. 1972. Ecosystem alteration by mosquito fish (Gambusia affinis) predation. Science, 175:539-618.

Jester, D.B., and B.L. Jensen. 1972. Life history and ecology of the gizzard shad, Dorosoma cepedianum (LeSueur) with reference to Elephant Butte Lake. New Mexico State Univ. Agricultural Exp. Station Research Report #218, 56 p.

Kalff, J. and R. Knoechel. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Ann. Rev. Ecol. Syst. 9:475-495.

Kajak, Z., I. Spodniewska, and R.J. Wisniewski. 1977. Studies on food selectivity of silver carp, Hypophtalmichthys molitrix (val.) on the plankton and benthos of the eutrophic lake. Pol. Arch. Hydrobiol. 22: 301-310.

Karasik, V.M. and V.N. Kondakov. 1974. Hydromechanical removal of seston from surface water. Hydrobiological Jour. 10: 85-86.

Keating, K.I. 1978. Blue-green algal inhibition of diatom growth: transition from mesotrophic to eutrophic community structure. Science, 199: 971-973.

Keating, K.I. 1981. Extracellular metabolite involvement in plankton community structure. pp. 146-197. In: Proc. of workshop on Algal Management and Control Tech. Rpt. #E-81-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. 313 pp.

Kerfoot, W.C. 1974. Net accumulation rates and the history of cladoceran communities. Ecology, 55: 51-61.

Koopman, B.L. and W.J. Oswald. 1977. Mechanical harvesting: Its new role in controlling water-blooms. Paper 21-8, 13 pp. In: Proc. 97th Ann. Conf. Amer. Water Works Assoc., Part II, Anaheim, CA.

Krupauer, V. 1971. The use of herbivorous fishes for ameliorative purposes in central and eastern Europe. Proc. Int. Symp. on Aquatic Weeds. Oxford. 3: 95-103.

Kutkuhn, J.H. 1957. Fertilization of plankton by juvenile gizzard shad in a shallow prairie lake. Trans. Amer. Fish Soc. 87-80-103.

Lamarra, V.A. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Verh. Internat. Verein. Limnol. 19: 2461-2468.

Lund, J.W.G., C. Kipling and E.D. LeCrew. 1958. The inverted microscope method of estimating algal numbers and statistical basis of estimations by counting. Hydrobiologia. II: 143-170.

Lynch, M. 1979. Predation, competition and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253-272.

Lynch, M. 1980. Aphanizomenon blooms: alternate control and cultivation by Daphnia pulex. pp. 299-304. In: W.C. Kerfoot (ed.). Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover. 793 pp.

Masters, M.J. 1971. The ecology of Chytridium deltanum and other fungus parasites on Oocystis spp. Can. J. Bot. 49:75-87.

McKellar, H.N. 1975. Metabolism and models of estuarine bay ecosystems affected by a coastal power plant. Ph.D. Dissertation, University of Florida, Gainesville, 270 p.

McKellar, H.N., and R. Hobro. 1976. Phytoplankton zooplankton relationships in 100-liter plastic bags. Contributions from the Asko Lab, University of Stockholm, Sweden, No. 13, 83 p.

Meinz, M. 1978. Improved method for collecting and transporting young American shad. Prog. Fish Cult. 40(4):130-131.

Moriarity, C.M. and D.J.W. Moriarity. 1973. Quantitative estimation of the daily ingestion of phytoplankton by Tilapia nilotica and Haplochromis nigripinnis in Lake George, Uganda. J. Zool., Lond. 171: 15-23.

Munro, J.L. 1967. The food of a community of East African freshwater fishes. J.Zool. 151: 389-415.

Odum, H.T., and C.M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publ. Inst. Mar. Sci. Univ. of Texas. 5:15-46.

Oswald, W.J. 1976. Removal of algae in natural bodies of water. Rpt. #76-1. Sanitary Engineering Research Laboratory, Univ. of California, Berkeley. 140 pp.

Padan, E. and M. Shilo. 1969. Distribution of cyanophages in natural habitats. Verh. Internat. Verein. Limnol. 17:747-751.

Paerl, H.W., M.M. Tilzer, and C.R. Goldman. 1976. Chlorophyll a versus adenosine triphosphate as an algal biomass indicator in lakes. J. Phycol. 12:242-246.

Pierce, R.J. 1977. Life history and ecological energetics of gizzard shad. Ph.D. Dissertation, Miami University, Ohio, 201 p.

Pollman, C.O., P.L. Brezonik, T.L. Crisman, and P. Sacco. 1980. Limnological studies on the Lake Apopka and the Oklawaha chain of lakes: 3. Water quality in 1979. Rept. to Florida Dept. Environ. Regulation, Tallahassee. Rept. No. ENV-07-80-02, Dept. Environ. Engr. Science, University of Florida, Gainesville, 109 p.

Porter, K.G. 1972. Methods for in situ study of zooplankton grazing effects on algal species composition and standing crop. Limnol. Oceanogr. 17: 913-917.

Porter, K.G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature. 244: 179-180.

Porter, K.G. 1975. Viable gut passage of gelatinous green algae ingested by Daphnia. Verh. Internat. Verein. Limnol. 19: 2840-2850.

Porter, K.G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. Science. 192:1332-1333.

Porter, K.G. 1977. The plant-animal interface in freshwater ecosystems. Amer. Scient. 65: 159-170.

Porter, K.G., M.L. Pace, and J.F. Battey. 1979. Ciliate protozoans as links in freshwater planktonic food chains. Nature. 277:363-364.

Prescott, G.W. 1962. Algae of the Western Great Lakes Area. Wm. C. Brown Co., Dubuque, Iowa, 977 p.

Prescott, G.W. 1981. A review of control measures for objectional algal "blooms." pp. 5-14. In: Proc. of Workshop on Algal Management and Control. Tech. Rpt. #E-81-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. 313 pp.

Rohde, W. 1958. Primaproduktion und Seetypen. Verh. Int. Verein. Limnol. 13: 121-141.

Safferman, R.S. 1973. Phycoviruses. pp. 214-237. In: N.G. Carr and B.A. Whitton (Eds.). The Biology of Blue-green Algae. Blackwell Sci. Pub.

Safferman, R.S. and M.E. Morris. 1962. Evaluation of natural products for algicidal properties. Appl. Microbiol. 10:289-292.

Safferman, R.S. and M.E. Morris. 1963. Algal virus: isolation. Science 140: 679-680.

Safferman, R.S. and M.E. Morris. 1967. Observations on the occurrence, distribution and seasonal incidence of blue-green algal viruses. Appl. Microbiol. 15: 1219-1222.

Schindler, D.W. and G.W. Comita. 1972. The dependence of primary production upon physical and chemical factors in a small senescing lake, including the effects of complete winter oxygen depletion. Arch. Hydrobiol. 69: 413-451.

Schuytema, G.S. 1977. Biological control of aquatic nuisances - a review. U.S. Environ. Protect. Agency, EPA-600/3-77-084. 89 pp.

Shapiro, J. 1979. The need for more biology in lake restoration. pp. 161-168. In: Lake Restoration. U.S. Environ. Protect. Agency, EPA 440/5-79-001. 254 pp.

Shilo, M. 1967. Formation and mode of action of algal toxins. Bacteriol. Rev. 31: 180-193.

Slobodkin, L.B. 1960. Ecological energy relationships at the population level. Amer. Nat. 94: 213-236.

Smith, A.O. 1971. Some aspects of trophic relation of gizzard shad, Dorosoma cepedianum (LeSueur). Proc. Okla. Acad. Sci. 148-151.

Tiffany, L.H. 1921. Algal food of the gizzard shad. Ohio J. Sci. 21(4): 113-122.

Tiffany, L.H. 1922. Some algal statistics gleaned from the gizzard shad. Science. 56: 285-286.

Tuschall, J.R., T.L. Crisman, P.L. Brezonik and J.N. Allinson. 1979. Limnological studies on Lake Apopka and the Oklawaha chain of lakes: 2. Water quality in 1978. Rept. to Florida Dept. Environ. Regulation, Tallahassee. Rept. No. ENV-07-78-01. Dept. Environ. Engr. Sciences, University of Florida, Gainesville.

United States Environmental Protection Agency. 1974. Methods for chemical analysis of water and wastes. U.S. EPA, Cincinnati, Ohio, 298 pp.

Vargo, G.A., P.E. Hargraves, and P. Johnson. 1975. Scanning electron microscopy of dialysis tubes incubated in flowing seawater. Marine Biology. 31: 113-120.

Van Duesen, R.D. 1974. Swans - beneficial and beautiful. Prog. Farmer (September): 82.

Velasquez, G.T. 1939. On the viability of algae obtained from the digestive tract of gizzard shad, Dorosoma cepedianum. Amer. Midl. Nat. 22: 376-405.

Wetzel, R.G. 1975. Limnology. W.B. Saunders Co., Philadelphia, 743 p.

APPENDIX A

GRAPHS OF CHANGES IN PARAMETERS OVER TIME FOR THE EXPERIMENTAL TANK STUDIES

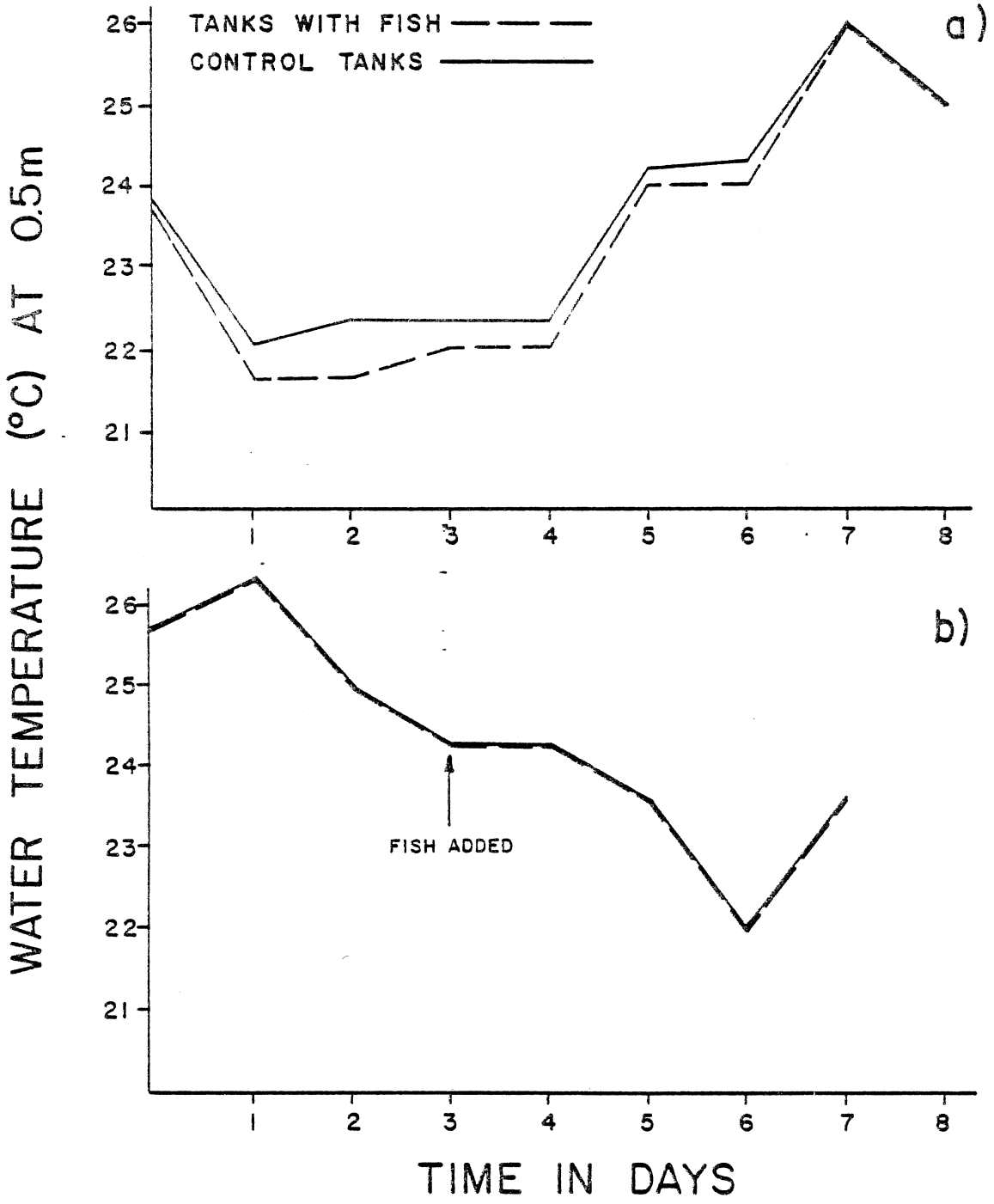

Fig. A-1. Changes in water temperature in tanks with and without shad at (a) natural stocking density (October 1979), and (b) high stocking density (May 1980.

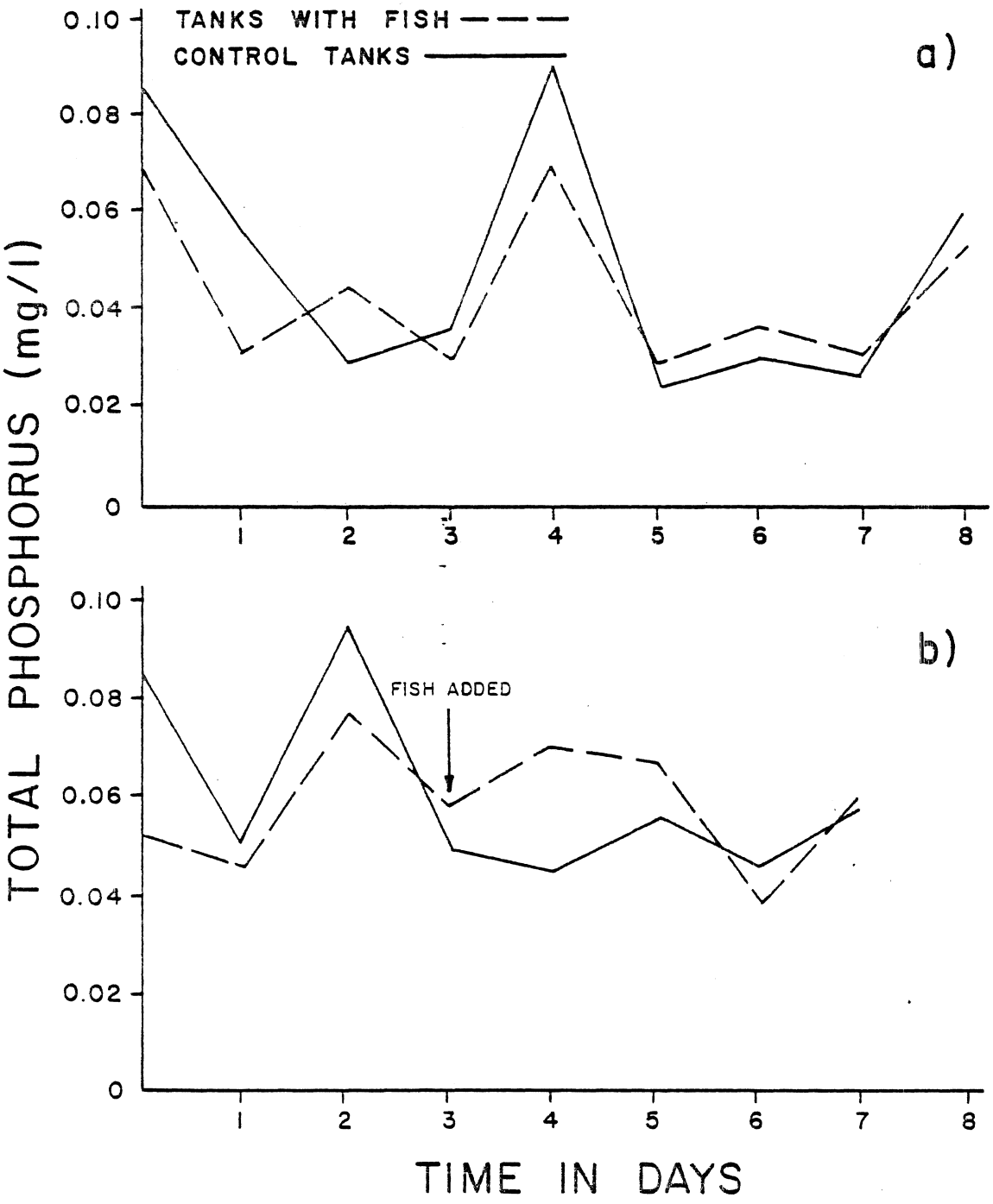

Fig. A-2. Changes in total phosphorus concentrations in tanks with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

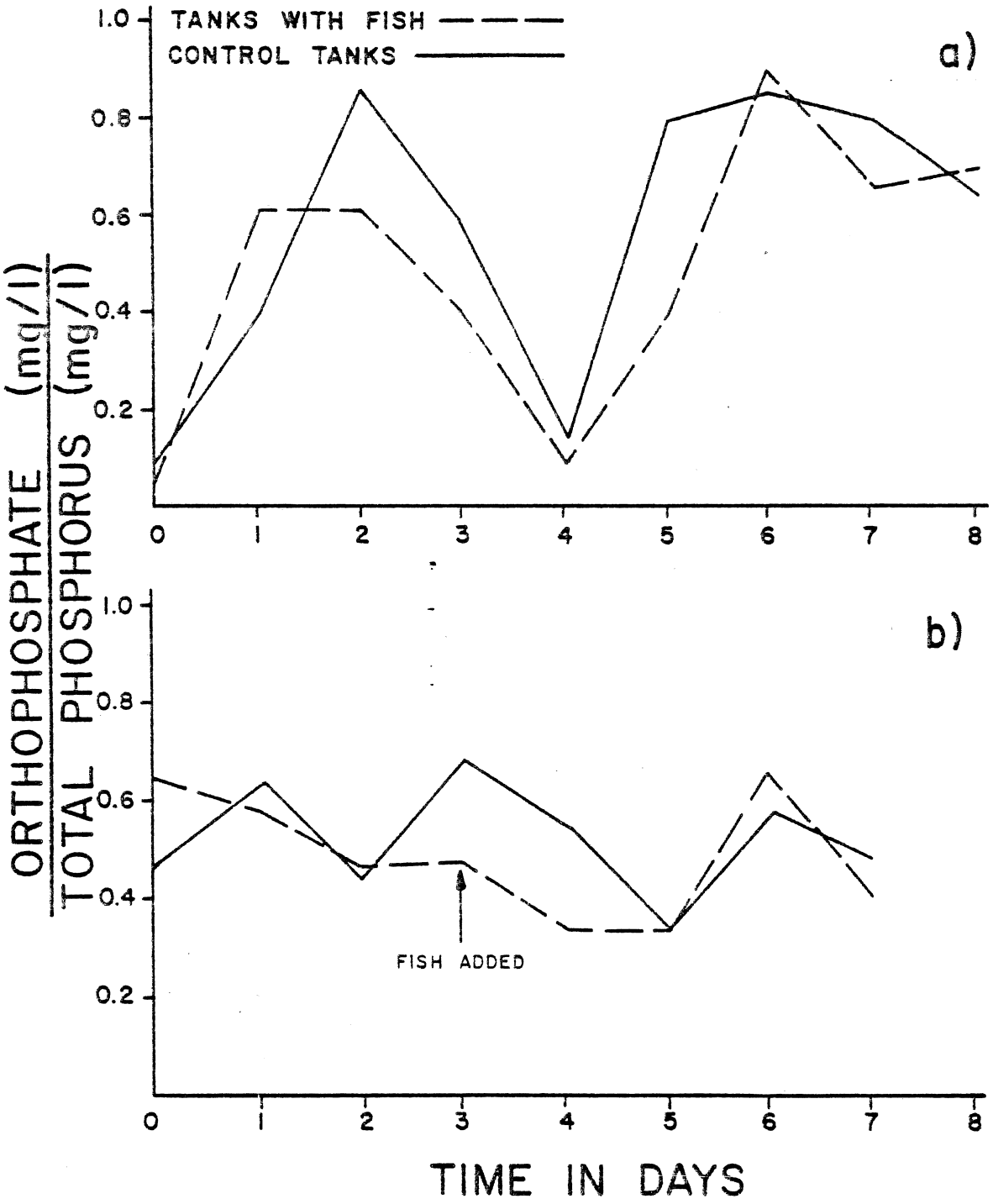

Fig. A-3. Changes in the ratio of orthophosphate to total phosphorus in tanks with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

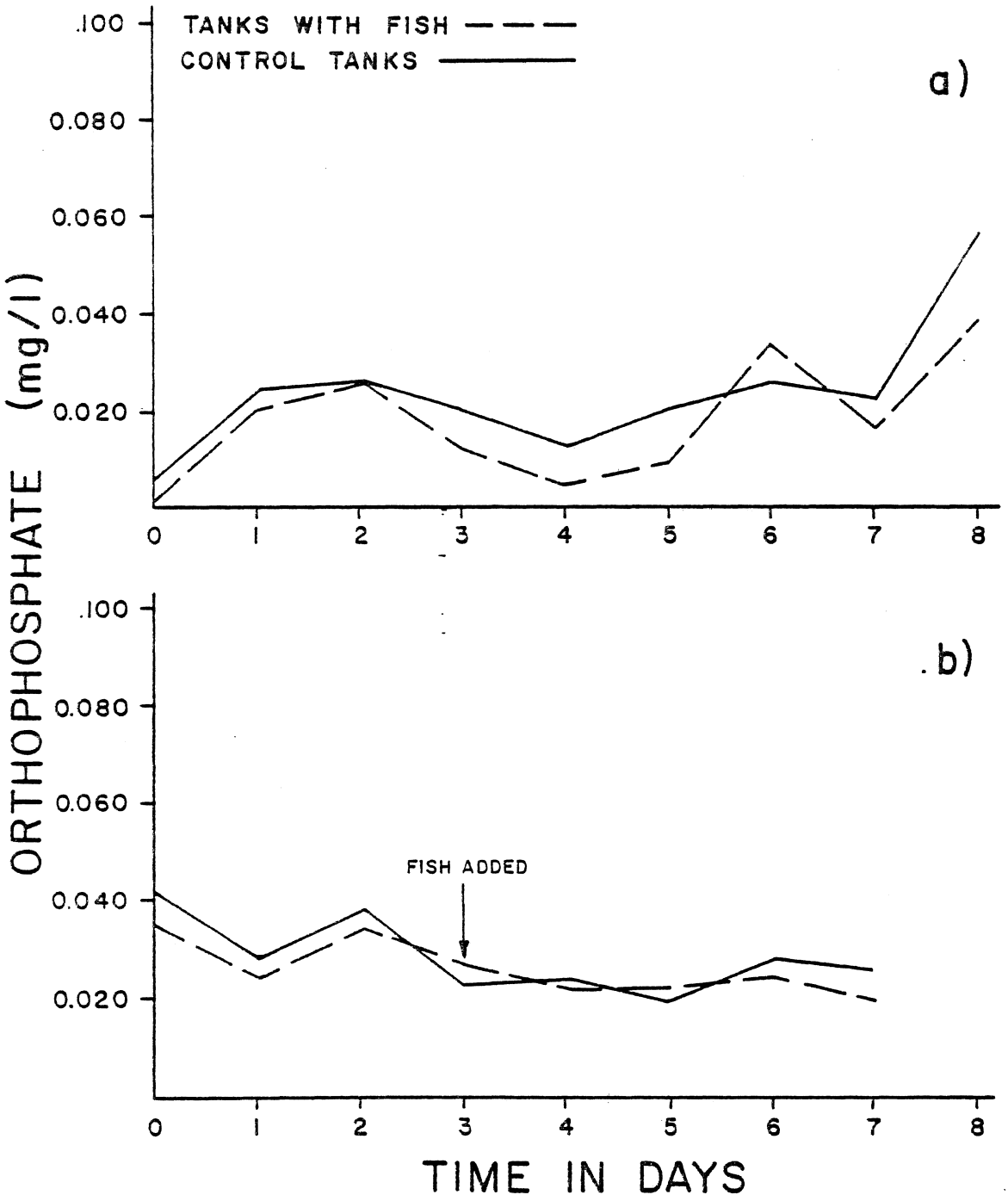

Fig. A-4. Changes in orthophosphate in tanks with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

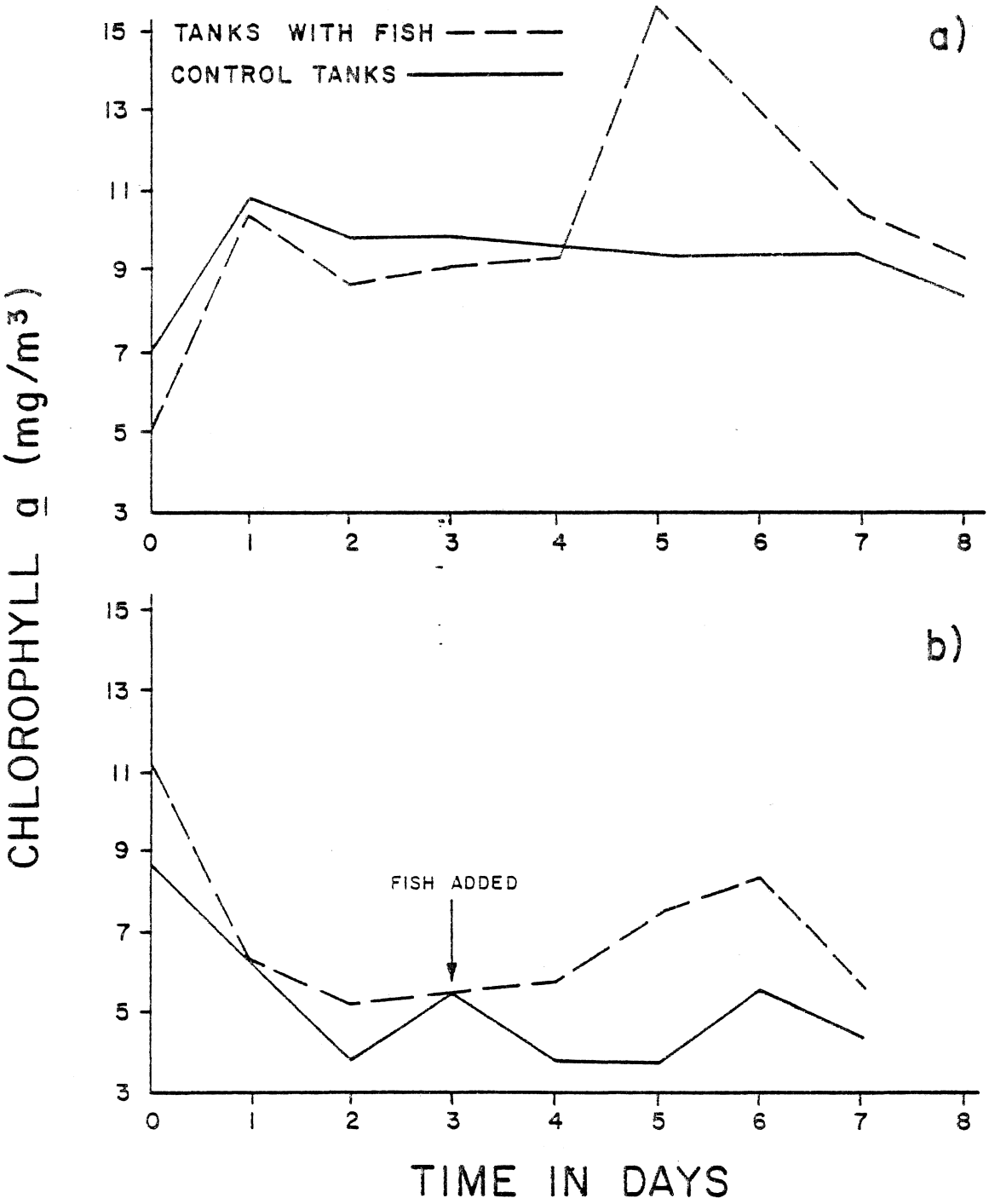

Fig. A-5. Changes in chlorophyll a concentrations in tanks with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

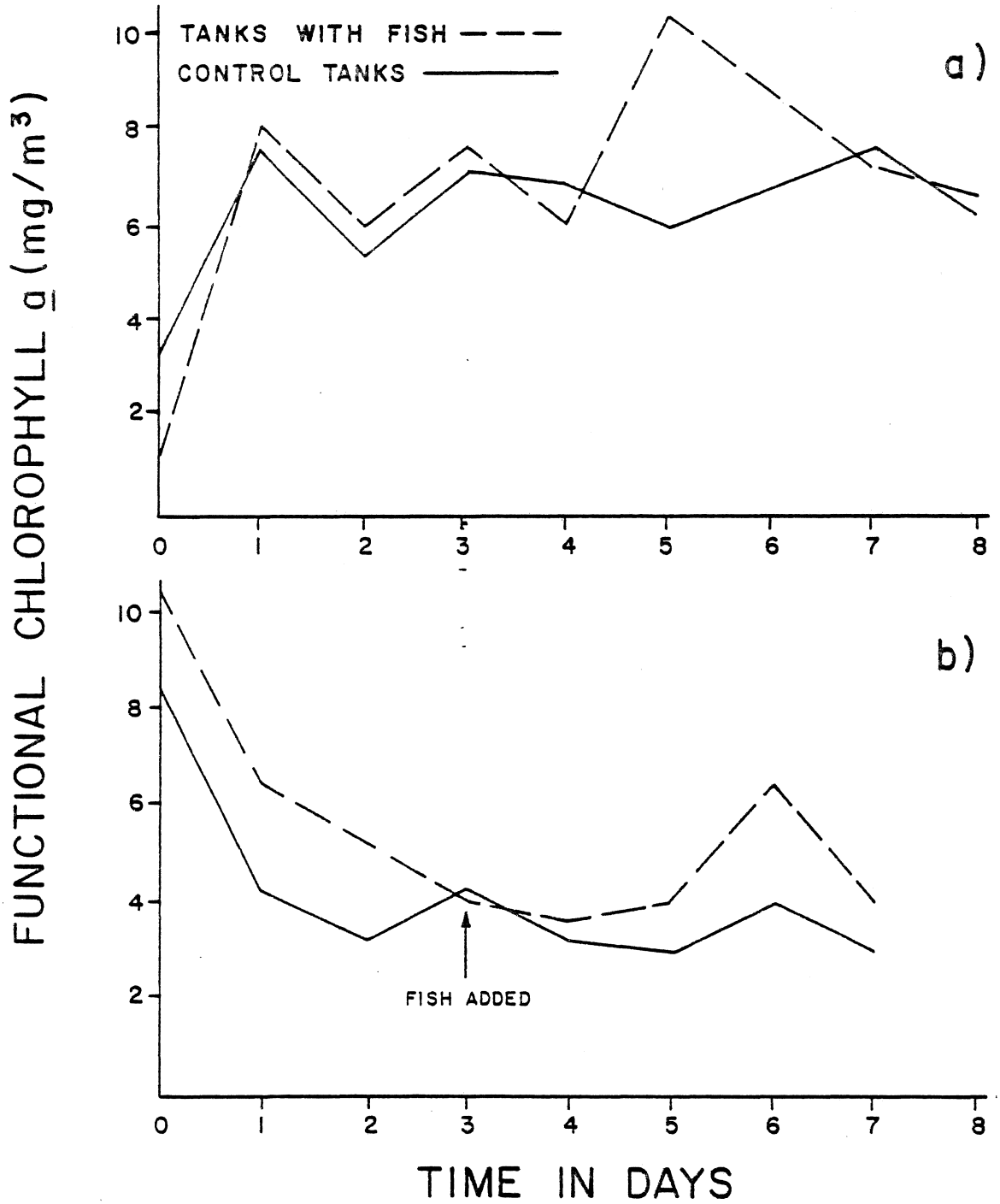

Fig. A-6. Changes in functional chlorophyll a concentrations in tanks with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

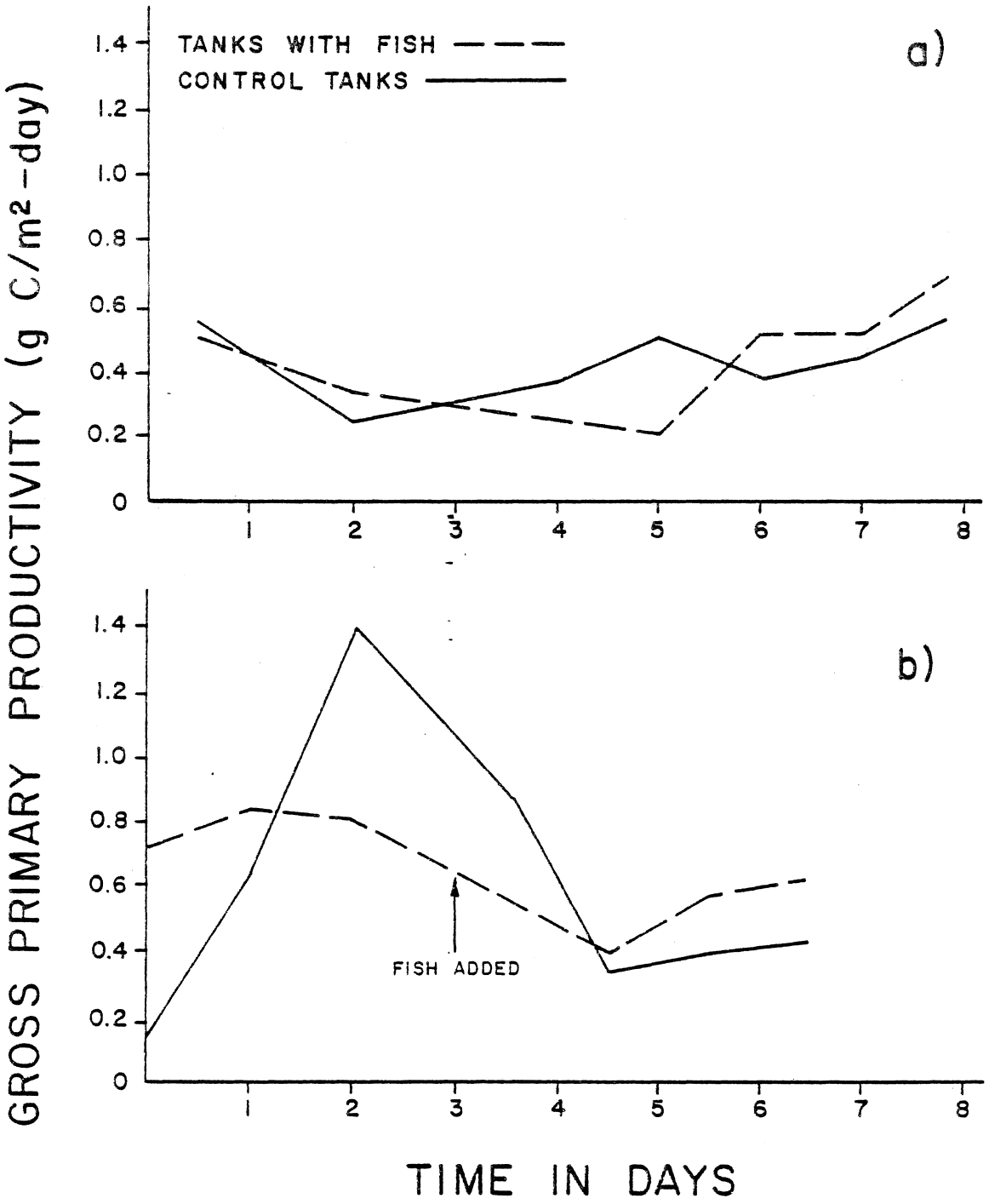

Fig. A-7. Changes in gross primary productivity in tanks with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

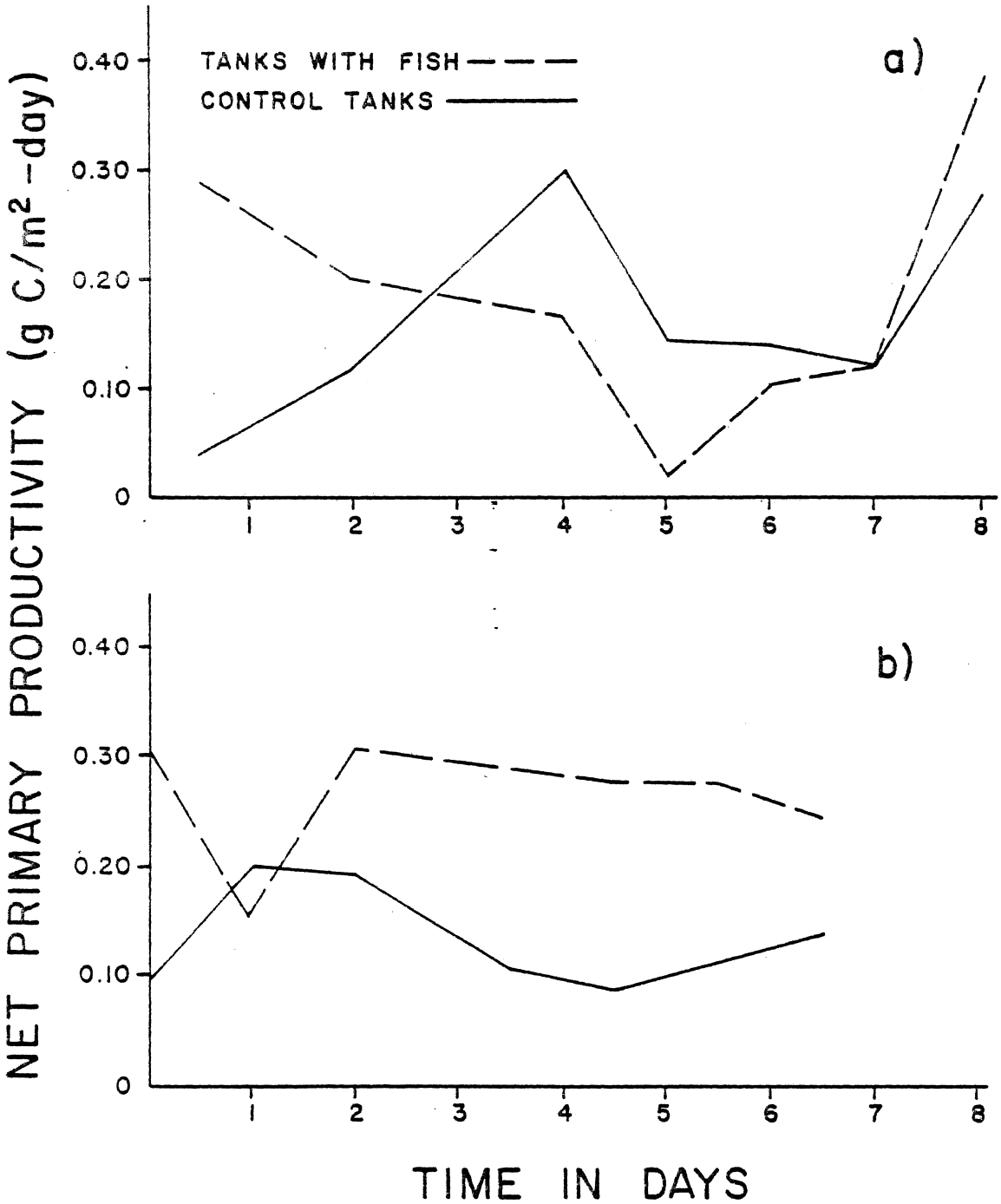

Fig. A-8. Changes in net primary productivity with and without shad at (a) natural stocking density (October 1979) and (b) high stocking density (May 1980).

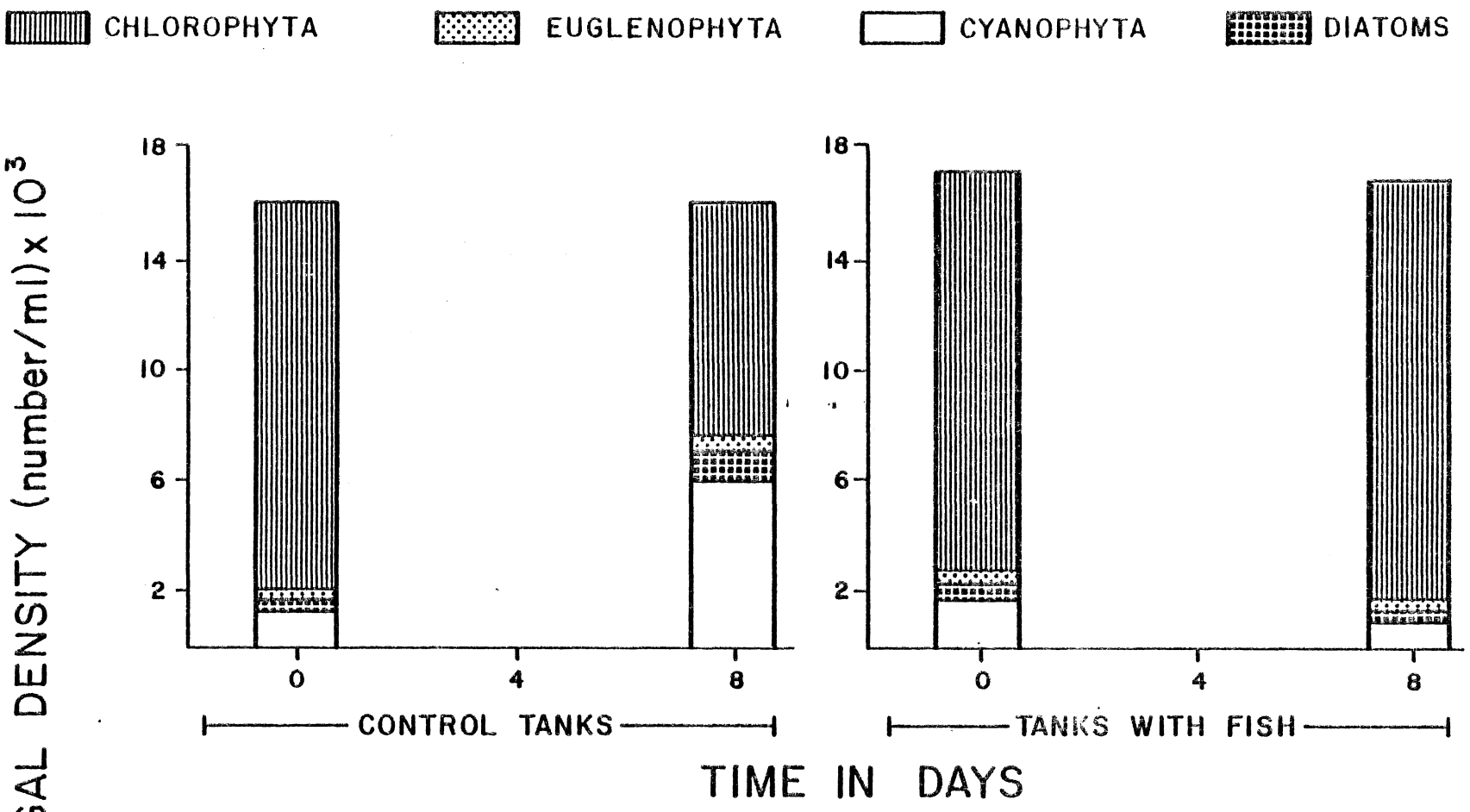

Fig. A-9. Changes in the density of algal dominants (#/ml) for the natural density stocking experiment.

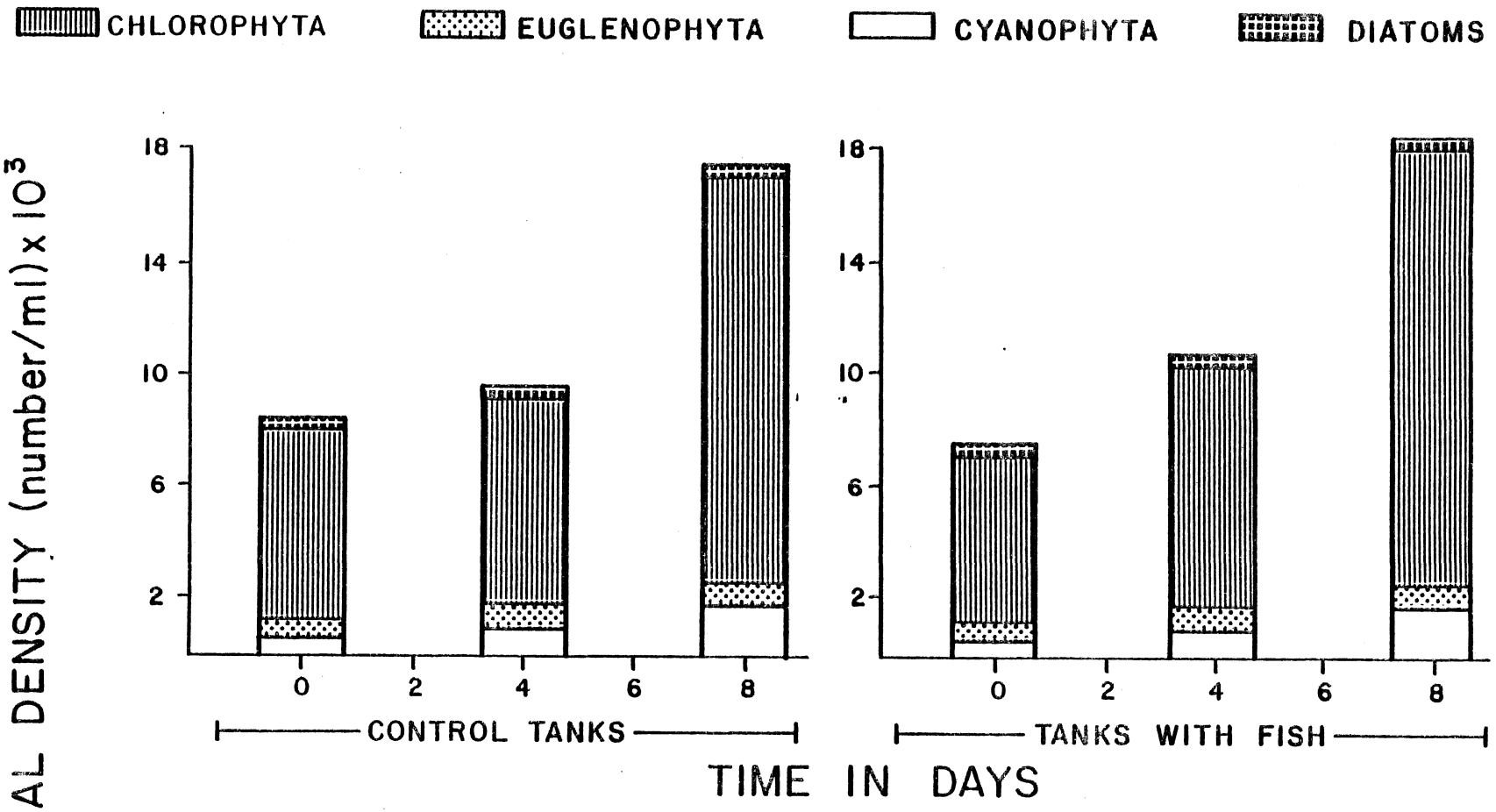

Fig. A-10. Changes in the density of algal dominants (#/ml) for the high density stocking experiment.

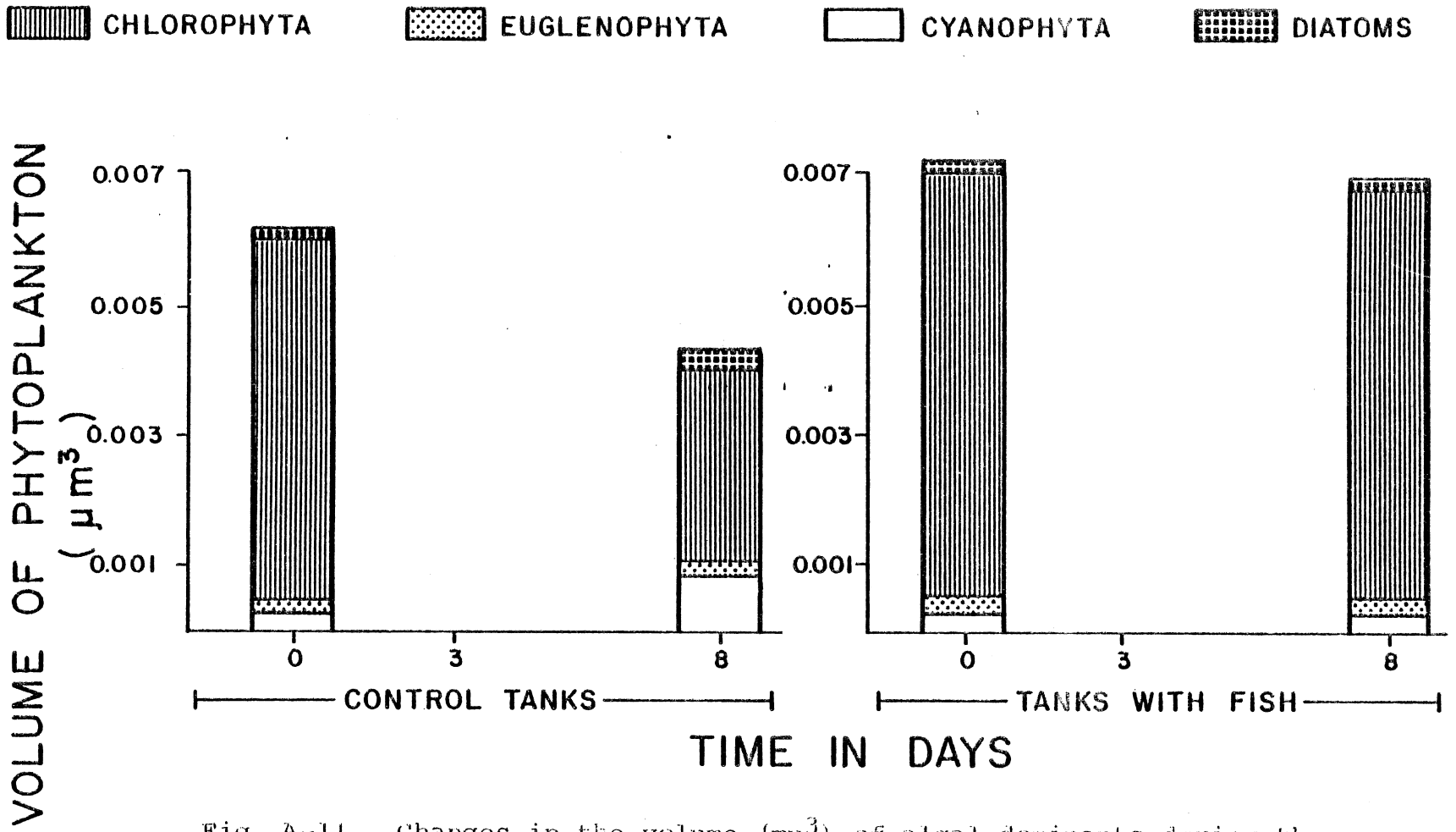

Fig. A-11. Changes in the volume ($m\mu^3$) of algal dominants during the natural density stocking experiment.

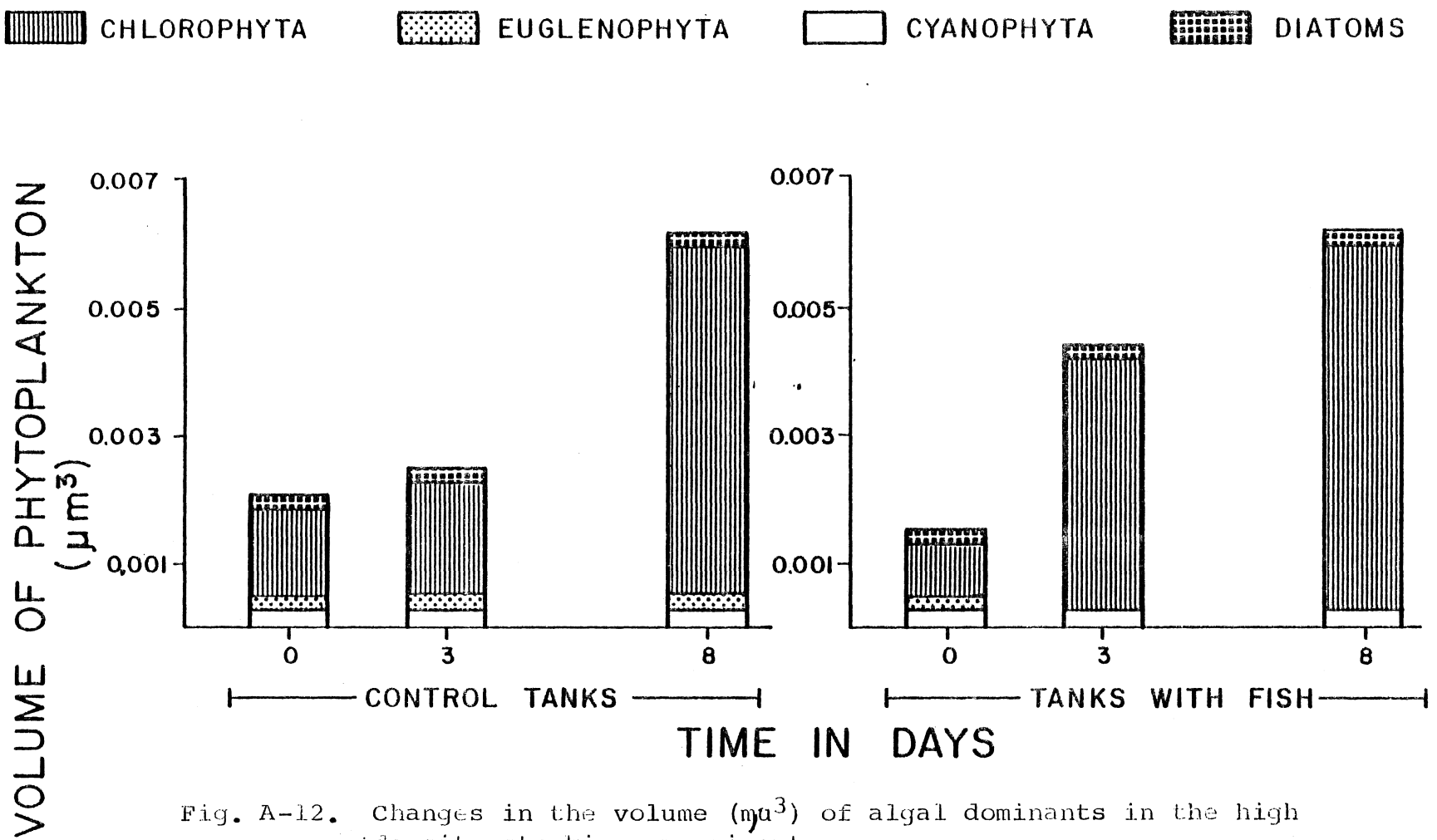

Fig. A-12. Changes in the volume (μm^3) of algal dominants in the high density stocking experiment.

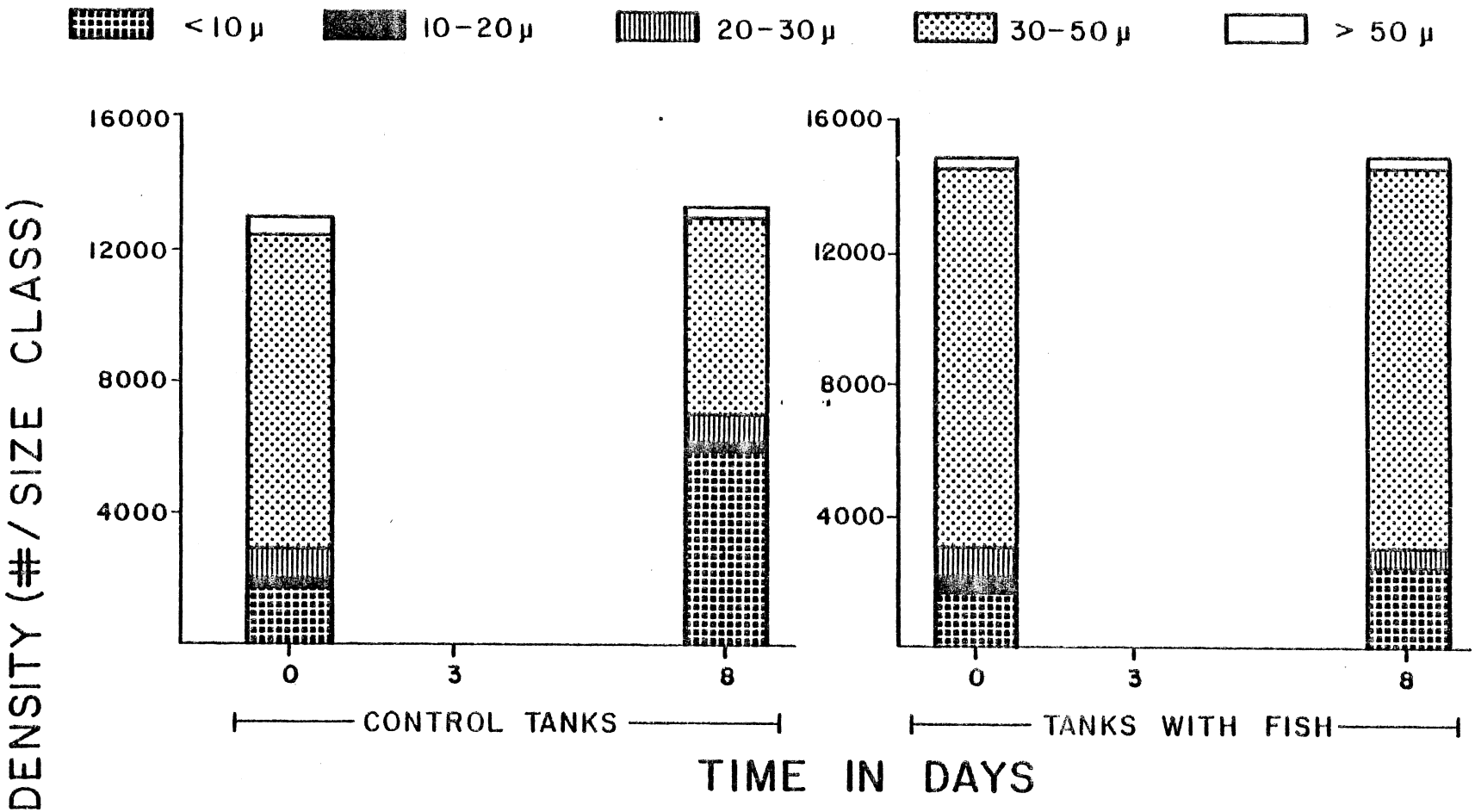

Fig. A-13. Changes in size classes of algal dominants during natural density stocking experiment.

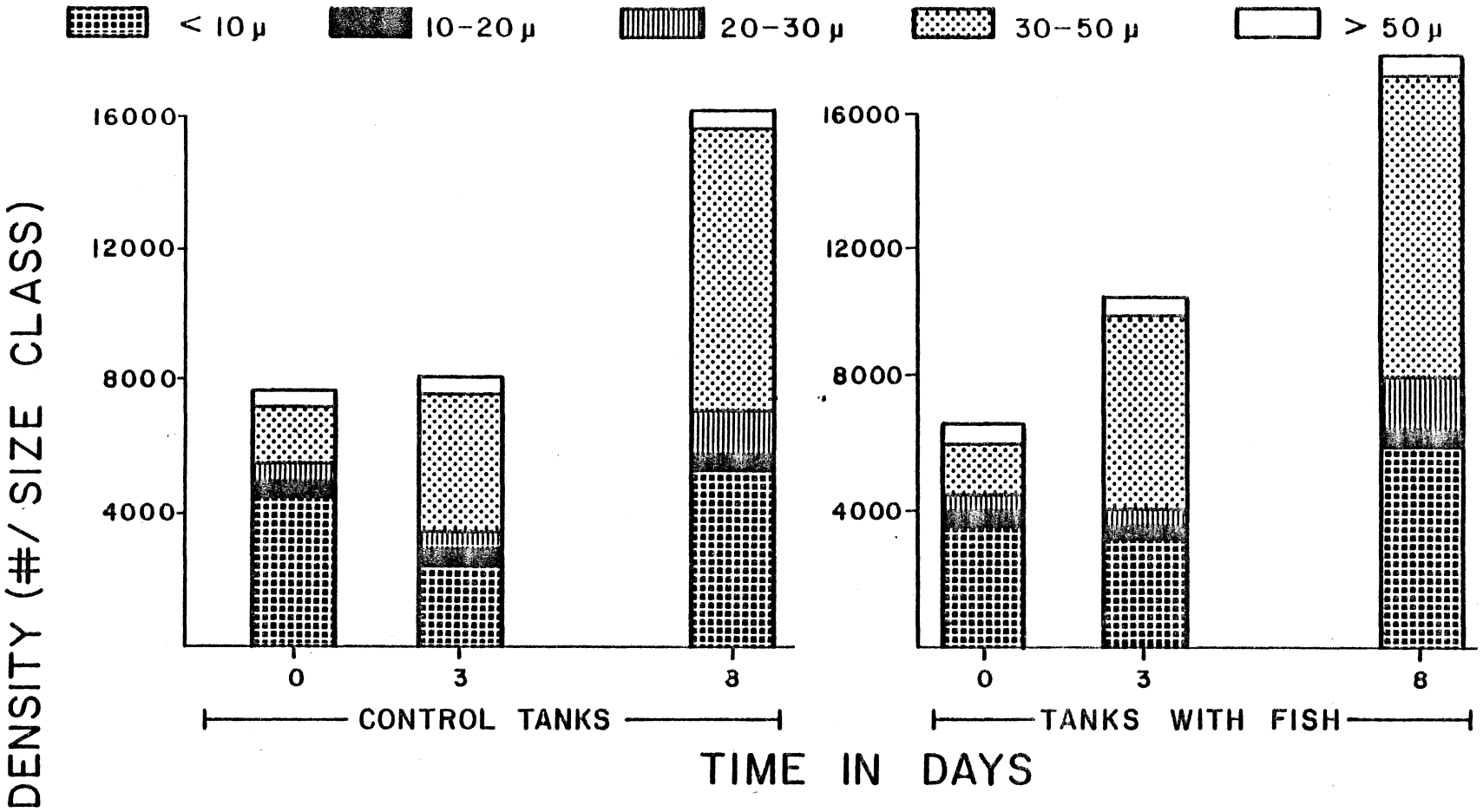

Fig. A-14. Changes in size classes of algal dominants during the high density stocking experiment.

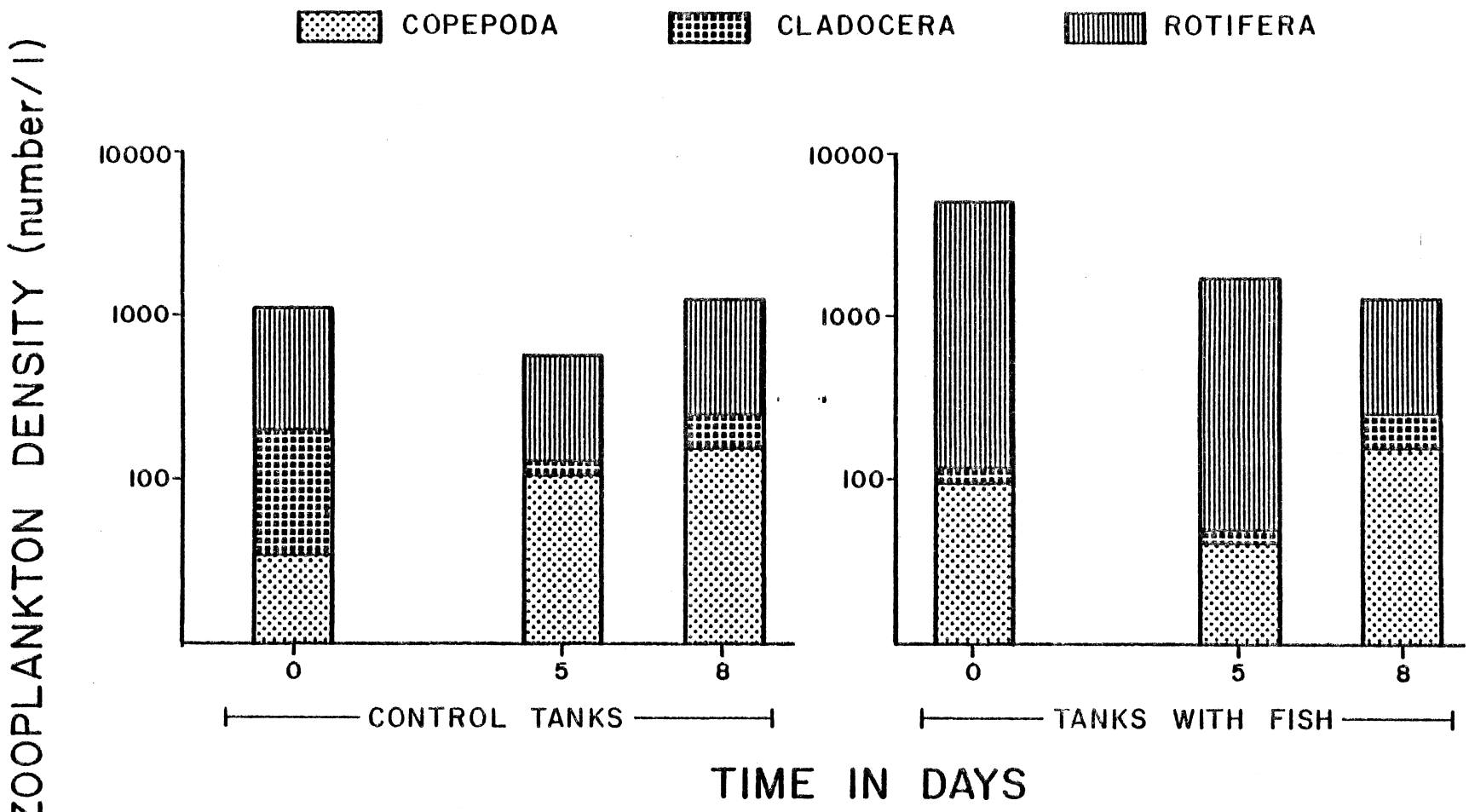

Fig. A-15. Changes in zooplankton densities during the natural density stocking experiment. Note that the y-axis is on a log scale.

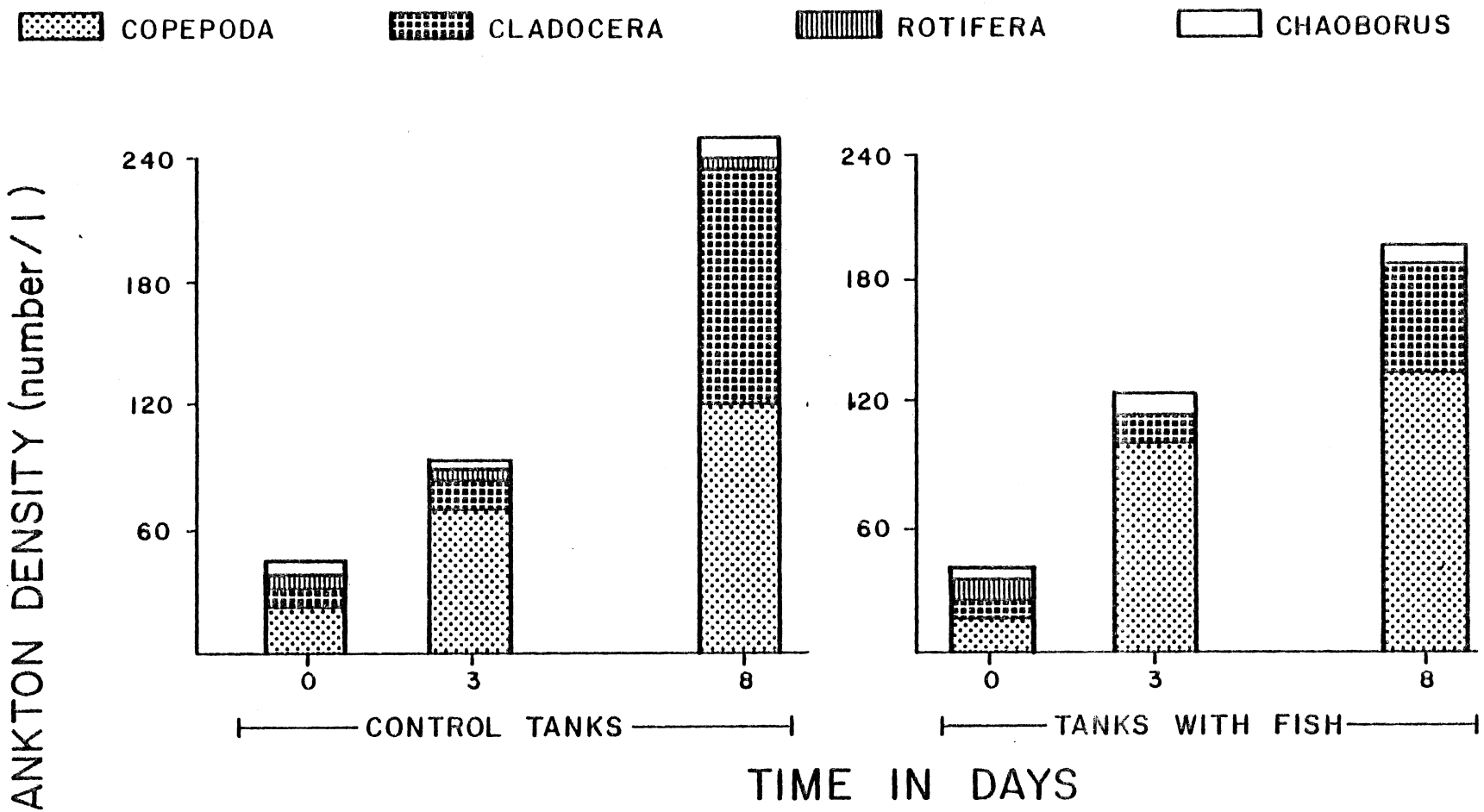

Fig. A-16. Changes in zooplankton densities during the high density stocking experiment.

APPENDIX B

CSMP PROGRAM

APPENDIX B

CSMP MODEL PROGRAM

```
* INTIAL CONDITIONS OF THE STATE VARIABLES; DA=DIGESTIBLE
  ALGAE
* IA=INDIGESTIBLE ALGAE, P=PHOSPHORUS, S=SHAD, Z=ZOOPLANKTON
* ALL VALUES ARE IN GRAMS CARBON/M2-MO
*
INCON ICDA= 645
INCON ICIA=2.16
INCON ICZ= 0.6417
INCON ICS=1.1214
INCON ICP=9.24E-2
*
* RATE COEFFICIENTS
*
CONST K1=1
CONST K2=2.7344E-3
CONST K3=.373
CONST K4=12.837
CONST K5=1
CONST K6=2.7344E-3
CONST K7=12.833
CONST K8=.3876
CONST K10=.8743
CONST K11=.1357
CONST K12=6.5
CONST K13=6.65
CONST K15=15.11
CONST K16=.1876
CONST K20=7.402E-3
CONST P1=.672
CONST P2=1.061
CONST RATIO=0.025
PARAM YRTIM=0.0
PARAM ZZ=0.0
PARAM PP=0.0
PARAM SS=0
PARAM DA1=0.0
PARAM IA1=0
```

```
PARAM PS=0
PARAM S1=0
PARAM Z1=0
*
* FUNCTION CARDS
*
* SOLAR RADIATION (JO) IS A VARIABLE FUNCTION "SUNLIT"
* THE FUNCTION CARD LISTS THE VALUES OF SOLAR RADIATION
* AS A FUNCTION OF TIME.  (KCAL/M2-MO)
FUNCTION SUNLIT=(0., 62.E3), (.083,71.4E3), (.167, 134,
8E3), (.25, 141.E3), (.33, 123.9E3), (.416, 120.E3),
(.5, 138, E3), (.583, 134.7E3), (.667, 114.E3), (.73, 106.
3E3), (.83, 71.4E3), (1., 62.E3)
*
*
* SINCE THE HALFSAT CONSTANT WILL VARY WITH THE CONCENTRA-
* TION OF P A FUNCTION TO ESTABLISH THE RELATIONSHIP IS USED
*
FUNCTION PHOS=(0., 0.025), (.005, .025), (.05, .1),
(.1, .1), (.2, .03)
*
FUNCTION SHAD=(0,0), (.2, 0.145), (.5, 0.174), (1.1, 0.2537),
(2.5, 0.1493), (3.9, .108), (6.0, .0001), (10.0, 1.E-6)
*FUNCTION TO LIMIT ZOOP FEEDING
FUNCTION ZOOP=(0,0), (.2, .01), (.4, 1.5), (.6, 5.44),
(.8, 4), (1., 1.2), (1.3, .12), (2, .001)
DYNAMIC
*
* FUNCTION GENERATORS
*
HAFSAT=AFGEN(PHOS,PP)
SUN=AFGEN(SUNLIT, YRTIM)
LIMEAT=AFGEN(SHAD, SS)
ZLIM=AFGEN(ZOOP, ZZ)
*
* DIFFERENTIAL EQUATIONS
*
DA=INTGRL(ICDA, GPDA-RESPDA-DAEATN)
      JO=SUN
      GPDA=((K2*JO*DA)/(1. +K1*DA+K5*IA))*(P/(HAFSAT+P))
      RESPDA=K4*DA
      DAEATN=K3*DA*S + K12*DA*Z
      DAEXCR=RATIO*RESPDA
```

```
*
IA=INTGRL(ICIA, GPIA-RESPIA-IAEATN+VIABIA)
      GPIA=((K6*JO*IA)/(1. +K5*IA+K1*DA))*(P/(HAFSAT+P))
      RESPIA= K7*IA
      IAEATN= K8*IA*S + K13*IA*Z
      VIABIA= K11*IA*S
      IAEXCR= RATIO*RESPIA

*
Z=INTGRL(ICZ, ZEATS-RESPZ-ZEATN)
      ZEATS= ZLIM*(IA+DA)*Z
      RESPZ= K15*Z
      ZEATN= K16*Z*S
      ZEXCR= RATIO*RESPZ

*S=INTGRL(ICS,SEATS-SRESP-APASS-SHARV)
      SEATS= LIMEAT*(IA+DA+Z)*S
      SRESP= K10*S
      SEXCR= RATIO*SRESP
      APASS=1.1*VIABIA
      SHARV=0.0

*
P=INTGRL(ICP,PLOAD+PIN-PUPTAK-POUT)
      PLOAD=P1
      PIN= DAEXCR+IAEXCR+ZEXCR+SEXCR
      PUPTAK=RATIO*GPDA + (RATIO*GPIA)
      POUT=P2*P
```